MIGRATION, DISPERSAL, AND SURVIVAL PATTERNS OF MULE DEER (*ODOCOILEUS HEMIONUS*) IN A CHRONIC WASTING DISEASE-ENDEMIC AREA OF SOUTHERN SASKATCHEWAN

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By

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ABSTRACT

Chronic wasting disease (CWD) has infected wild deer of Saskatchewan for at least the past 10 years. Disease management plans have evolved over the years, but without information on mule deer (*Odocoileus hemionus*) habits and movements in the grasslands of southern Saskatchewan. We radio-collared and monitored the survival and movements of 206 mule deer from 2006 to 2009. Long distance movements by deer have potential to transfer disease to previously naïve areas. Survival rates had not yet been evaluated in this area; baseline data will provide a useful measure for population-level impacts of the disease in the future.

Juvenile dispersals and adult migrations were contrasted from 4 study areas along the South Saskatchewan River. Dispersal distance (median = 22.8 km, n = 14) was similar to migration distance (median = 16.0 km, n = 49). Median migration distance was similar between males (15.7 km, n = 51) and females (19.7 km, n = 65). Obligatory migrants were more likely to be female. Deer from an area of extensive grassland were more likely to be migratory than their counterparts in fragmented grassland of an agricultural landscape. Maximum migration and dispersal distances were 113 km and 195 km, respectively. Movement paths of 33 GPS-collared deer were best explained by high terrain ruggedness values and proximity to grassland.

Seasonal survival rates showed that deer had lowest survival in autumn months during hunting season. Juveniles had lower survival than adults in all seasons. Harvest regime changes in 2008 improved the autumn survival of adult females but adult males had lower survival than in 2007. Body condition of captured deer was evaluated from residuals of mass-length regression. Cox regression analyses suggested that deer in good body condition (75^{th} percentile) were half as likely to die and that those in very poor body condition (10^{th} percentile) were twice

as likely to die. Radio collars that weighed > 2% of body mass negatively affected survival and we recommend future researchers take this into consideration.

Survival, dispersal, and migration rates and patterns are crucial parameters in modeling CWD in local mule deer populations. Saskatchewan wildlife managers aim to prevent CWD spread into new areas, and can use mule deer movement orientations to target surveillance accordingly. White-tailed deer (*Odocoileus virginianus*) movements are briefly discussed; further knowledge of their movements is required for CWD management in all of Saskatchewan.

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LIST OF ABBREVIATIONS

AD	Adult
AIC	Akaike information criterion
ANT	Antelope Creek study site
BEEMAT	Beechy and Matador pasture study site
BCI	Body condition index
CCWHC	Canadian Cooperative Wildlife Health Centre
CWD	Chronic wasting disease
DOU	Douglas Park study site
SWI	Swift Current Creek study site
F	Female
GEE	Generalized estimating equation
GIS	Geographic information system
GPS	Global positioning system
JUV	Juvenile
KDE	Kernel density estimate
M	Male
MOE	Ministry of Environment
QIC	Quasi-likelihood under independence model criterion
QICC	Corrected quasi-likelihood under independence criterion
S.S. RIVER	South Saskatchewan River
TRI	Terrain ruggedness index
VHF	Very high frequency

CHAPTER 1
INTRODUCTION AND LITERATURE REVIEW

1.1 Chronic Wasting Disease

Chronic wasting disease (CWD) is a fatal transmissible spongiform encephalopathy (TSE) that affects wild and domestic cervids of North America. Like other prion diseases, it is characterized by chronic neurodegeneration, loss of motor skills, and certain fatality as a result of a protease-resistant isoform of cellular prions (PrP^{res}) that accumulate in the host central nervous system (CNS) and lymphatic tissues. Unlike most prion diseases (except scrapie), CWD can be transmitted by environmental contamination (Mathiason et al. 2009) and like scrapie is transmitted horizontally. Prions are found in bodily fluids (saliva, blood, urine) and excrement (Mathiason et al. 2006), muscle tissue, and carcasses (Miller et al. 2004). Prions are notably resistant to degradation in the environment (Johnson et al. 2006, Wiggins 2009). Disease spread is relatively slow but persistent (Bollinger et al. 2004); once established in an area, eradication of CWD has so far proven to be impossible. North American wildlife managers have struggled to understand, manage, and geographically contain the disease for over 4 decades. It was first documented in captive mule deer at a research facility in Colorado in 1967 and in free-ranging elk of the same state in 1981 (Williams and Miller 2002). By early 2010, CWD was found in 17 states and 2 provinces.

1.1.1 CWD in Saskatchewan

A mule deer (*Odocoileus hemionus*) shot in 2000 in western Saskatchewan was the first Canadian wild cervid to be detected with CWD. White-tailed deer (*Odocoileus virginianus*) now

account for a growing portion of CWD-positives in provincial surveillance and the disease was recently detected in wild elk (Canadian Cooperative Wildlife Health Center (CCWHC), unpublished data). Other cervid species of Canada susceptible to the disease include black-tailed deer, moose (*Alces alces americanus*) and potentially caribou (*Rangifer tarandus*) (Happ et al. 2007).

Wildlife management is improved by scientific knowledge of local populations, but disease outbreaks often require timely decisions by wildlife managers, often with incomplete knowledge of important factors related to the ecology and epidemiology of the disease (Schauber and Woolf 2003). Geographic spread of CWD can be predicted by host animal movement (Miller et al. 2000). Mule deer life habits, including movement patterns, migration, dispersal, and survival rates, vary by region and there are currently no publications on these topics in the Canadian Prairies. The need for site-specific research in Saskatchewan arose in 2000 when CWD was first detected in wild mule deer.

At that time, managers decided to reduce deer density where the positive was found and to sample adjacent areas—an action plan similar to those already in place in areas of Wisconsin and Colorado. The herd reduction program relied on hunter participation in the Earn-a-Buck program: hunters were required to submit 2 antlerless (doe or fawn) heads in order to receive an either-sex tag. The either-sex tag was usually used to harvest an adult male. Management efforts have failed to eradicate the disease and in 2008 the Ministry of Environment made a decision to shift focus from eradication to monitoring and reducing prevalence and minimizing spread throughout the province. CWD was now considered enzootic in some areas.

At the time of this research project's proposal, there was speculation that the Earn-a-Buck management program, by encouraging harvest of females and adult males, was skewing local

population age/gender ratios toward higher proportions of juvenile males. Since juvenile males are reportedly more likely to disperse, it was argued the program was likely increasing geographic spread of disease. In response to these criticisms alterations were made to Earn-a-Buck regulations allowing harvest of 3-point-or-less males, as well as females. This change likely reduced the proportion of juvenile males in CWD control areas; nevertheless, the role of dispersal in disease spread remained worthy of investigation. Young male deer are the highest risk group for CWD infection (Osnas et al. 2009) and are also most likely to disperse (Kammermeyer and Marchinton 1976, Dobson 1982, Nixon et al. 1994). These facts, in addition to their often high numbers within a managed deer population, make juvenile males arguably of utmost concern for geographic spread of CWD. During the pilot year of this study (2006), long distance migrations were commonly observed at one study area. The role of migratory deer in the geographic spread of disease across the landscape came into consideration.

1.1.2 CWD Management Challenges

CWD management programs for wild deer have developed rapidly over the past 20+ years in North America but clear evidence of efficacy has been difficult to demonstrate. The programs mainly involve some form of deer cull through increased hunter harvest or sharp-shooting. At the 3rd International CWD Symposium in 2009, a common concern expressed by state and provincial wildlife managers was the decline of public support and diminished funds for CWD management programs. Wildlife disease management programs are long-term investments, and due to the slow spread and long time-course of CWD, detecting changes in prevalence and distribution is difficult (Conner et al. 2008). Valid scientific assessment of the efficacy of reducing deer density on CWD prevalence requires a large sample size and many years of data (Conner et al. 2007). CWD management programs involving herd reduction are

controversial and are further complicated by the uncertain implications of CWD for wildlife, domestic animal and human health (Williams and Miller 2002, Vaske 2010).

While funding and support may be declining, research activities over the past decade have contributed a great deal of knowledge about CWD and managers have more tools to understand and predict its transmission. With this knowledge the scientific community, wildlife managers, and hunters can collaborate to innovatively manage deer and CWD. Advanced spatio-temporal analyses, disease modeling, and lessons learned from the past will aid in efficient allocation of funding to disease management programs. For example, Illinois has found a significant decreasing trend of CWD prevalence in young deer where sharpshooting was implemented for a number of years (Shelton et al. 2009).

Despite the challenges, CWD management programs continue because long-term effects of the disease on wild populations are still unknown. In discrete areas, prevalence can be quite high; it has been documented at >30% (Miller et al. 2008) in Colorado mule deer. Realizing eradication is no longer a reasonable goal, many wildlife agencies (including Saskatchewan's Ministry of Environment) have shifted focus toward disease prevention in new areas, and monitoring areas where it is currently found.

1.2 Literature Review

1.2.1 Study Species: Mule Deer (*Odocoileus hemionus*)

The mule deer is a North American cervid found in the western half of the continent, extending in the south from Mexico and north into the Yukon of Canada. The species evolved in the grassland and rugged badlands of the prairies and foothills of the Rocky and Sierra Mountain ranges. Also known as black-tailed deer, there are 7 subspecies of *O. hemionus* recognized and 4 more debated (Mackie et al. 2003). The most widespread subspecies, the Rocky Mountain mule

deer (*O. hemionus hemionus*), is found in the mid-western United States and Canadian provinces of Alberta, British Columbia, and Saskatchewan.

Mule deer share much of their range with their North American counterpart—the white-tailed deer—that evolved in the deciduous forest areas of the east. They are easily distinguished by their appearance and behavioral traits. Distinguishable characteristics include size, color and shape of the tail, antler form, ear size, metatarsal gland size, and the mule deer's distinctive stotting gait—a 4-footed bound used to quickly navigate rugged terrain. They stott when threatened, using precise movements to place themselves somewhere in their surroundings that will provide cover or an obstacle to evade predators. White-tailed deer flee danger by quickly running for the nearest cover, and so proximity to woodland cover is a more essential habitat requirement than for mule deer.

1.2.1.1 Habitat preferences

Mule deer range extends across a number of ecoregions including semi-arid desert, prairie, and mountain foothills; thus, they are adapted to a number of habitat types. Most often they are associated with rugged terrain including steep slopes of mountainous areas, badlands, and river breaks. The terrain may be shrub-covered, semi-forested, or open grassland.

Mule deer feed on herbaceous materials including leafy forbs, shrubs, and grasses, as well as some browse (woody materials). Kufeld et al. (1973) listed 788 species of plants eaten by Rocky Mountain mule deer (in Mackie et al. 2003). Mule deer acquire water from food sources as well as free-water sources. They generally stay within a few kilometers of open water, and females are more likely to be near water. In drought periods, fawn production is lower (Lawrence et al. 2004).

1.2.1.2 Breeding & social structure

Deer are organized in matrilineal groups, with 2 or more generations of females in family groups. The dominant or matriarch deer is a mature dam with successful reproductive history (Hawkins and Klimstra 1970, Kucera 1978, Porter et al. 1991). Social organization varies seasonally. Sexual segregation is common for all seasons except winter, when both sexes are found in large groups on wintering range. During parturition, does isolate themselves to rear their fawns (Ozaga et al. 1982). In the fall, they may reunite with previous offspring and other female groups. Males tend to range in different areas than females and form buck groups (Mackie et al. 2003). Females exhibit more fidelity to their home ranges than do bucks (Geist 1994b).

Mule deer are polygynous breeders, but males tend to an individual female for short periods until she is bred. Most begin breeding after the age of 1.5 years, and large bucks are dominant breeders. The breeding period varies by location but is generally in autumn and early winter; in Saskatchewan, breeding usually peaks in mid-November.

1.2.1.3 Importance to society

Mule deer provide aesthetic, recreational, and economic benefits to society and are important species in ecosystem health. As large and abundant herbivores, they affect vegetation composition and structure and are important to nutrient cycles (Augustine and McNaughton 1998). Deer are valued for recreation that is consumptive (i.e., hunting) as well as non-consumptive (e.g., sight-seeing or photography). Recreational users are willing to pay to hunt or just see deer (Conover 1997). They can also have economic cost through crop depredation, landscape damage, and vehicle collisions (Kie and Czech 2000, Côté et al. 2004)

In Saskatchewan, big game species (including mule deer, white-tailed deer, elk, moose, and black bears) are the primary choice of hunters. An economic evaluation of hunting in Saskatchewan estimated annual expenditure by big-game hunters at over $30 million (Derek

Murray Consulting Associates 2006). Known presence of CWD in local deer is likely to alter hunter behavior or participation (Miller and Shelby 2009), in turn affecting local and wildlife agency revenue generated by hunters (Needham and Vaske 2008).

1.2.2 Dispersal

Dispersal is a means of genetic exchange essential to a species' fitness. Local population dynamics are a function of additions (births and immigrations) and losses (deaths and emigrations). Despite its essential role in populations, dispersal is relatively poorly understood. Much of the literature on North American deer movements refers to studies on white-tailed deer in the United States. Deer dispersal is defined as a permanent movement away from the individual's natal range, and is usually undertaken by yearling males. Dispersal reduces inbreeding and resource competition (Kammermeyer and Marchinton 1976, Holzenbein and Marchinton 1992, Wolff 1993, Rosenberry et al. 2001).

Previous mule deer studies report high fidelity to annual or seasonal home ranges (Garrott et al. 1987, Kufeld et al. 1989). In Montana, emigration rates were high in juvenile males (16 of 24), low in juvenile females (1 of 29), and occasional in adults. Distances varied from 11 to 140 km (Wood et al. 1989). Sixty per cent of male and 35% of female yearlings dispersed in a mark-recovery study in Utah (Robinette 1966). Dispersal distances of black-tailed deer (*Odocoileus hemionus columbianus*) in British Columbia and Washington averaged 15.2 km for males and 12.2 km for females (Bunnell and Harestad 1983).

A study in Pennsylvania documenting dispersal of 308 juvenile male white-tailed found population densities had no effect on dispersal distance or rate, but that landscape characteristics affected dispersal distance. Dispersal distance was greatest in areas of least forest cover (Long et al. 2005). Harvest-induced alterations of the sex ratio within the population seemed to play a role in the seasonality of dispersal. Although the overall dispersal rate was not affected, autumn

dispersal increased when density of adult males increased, and spring dispersal decreased along with lower density of adult females (Long et al. 2008). The authors also found that spring-time dispersals were of longer distances than autumn dispersals, and they suggested inbreeding avoidance behavior required longer distances than did mate competition. Average dispersal distance was 4.6 km and maximum distance was 8.3 km.

Average dispersal distances in other white-tailed deer studies varied from 3 km in Virginia (Holzenbein and Marchinton 1992) to 38 km in Illinois (Nixon 1994). The maximum distance recorded was 212 km in South Dakota (Kernohan et al. 1994). In contrast, Saskatchewan white-tailed deer emigration distances have been recorded at a mean 215 km and maximum of 672 km (Stewart and Runge 1985).

1.2.3 Migration

Migration is seasonal movement between non-overlapping ranges. Deer in northern climates or mountainous areas tend to migrate as an adaptation to cold weather conditions or changes in seasonal resource availability (Nelson and Mech 1984, Garrott et al. 1987, Sabine et al. 2002). Migratory deer have potential to spread disease across landscapes. Seasonal home ranges may be relatively small, but long distances between seasonal ranges may result in coverage of a large area. Seasonal home ranges of groups of deer may overlap resulting in increased contact among groups of deer and the potential for long distance disease spread. In addition, migratory deer may have seasonal ranges in different wildlife or disease management areas (Brinkman et al. 2005). Migratory behavior of mule deer in Saskatchewan has not been previously documented and these data provide insight into potential contact routes for disease transmission.

Migration strategies vary by ecoregion. In mountain foothill regions, mule deer typically migrate from high summer elevations when forage is abundant, to the protective foothill and

basin ranges in winter. At the eastern edge of their range in the prairies, mule deer are usually non-migratory and inhabit patchy environments along river drainages. The rugged topography is used as cover to avoid predators and for protection from severe weather (Mackie et al. 2003). Mixed migration strategies have been observed in local populations and have been attributed to variable climatic conditions (Nicholson et al. 1997).

Mule deer in a CWD-endemic area of Colorado were much more likely to migrate than disperse, and the authors suggest that exchange of individuals between population units occurred most often in the summer months. Only 3 of 151 deer (2%) dispersed, at a distance of 7 to 15 km. The average migratory proportion of the deer studied was 52% but varied between population units and the average distance was 27.6 km (SE = 1.4) (Conner and Miller 2004). A previous study in northwest Colorado found 100% of female mule deer migrated an average distance of 27 km (Garrott et al. 1987). In Wyoming, Sawyer et al. (2005) found a high rate and distance of migration: 95% of the 166 collared (mostly female) mule deer migrated an average distance of 84 km (range 20–158 km).

1.2.4 Survival

Survival rates are essential information in population dynamics and management. Causes of mortality include hunting, predation, disease, malnutrition, winter severity, vehicle collisions, interspecific competition and habitat loss or change (Wood et al. 1989, White et al. 1987, Unsworth et al. 1999, DelGiudice et al. 2002). Miller et al. (2008) found that prion-infected deer (n = 57) were 3.84 times more likely to die (95% CI: 1.64–8.99) than their uninfected counterparts, and that mortality from mountain lion (*Puma concolor*) predation was higher than expected. In order to assess the impact of CWD on Saskatchewan deer populations in the future, knowledge of present survival trends must be measured for comparison. In addition, seasonal survival rates provide insight on the effects of the herd reduction program in the study area.

This research project was not designed to assess causes of mortality as radio-tracking was too infrequent. Typically carcasses when found were scavenged and a cause of death could not be determined. Predators of deer commonly observed in southern Saskatchewan include coyotes (*Canis latrans*) and domestic dogs (*Canis lupus familiaris*). Runge and Wobeser (1975) surveyed winter mortality of deer in Saskatchewan, and found that when predation was the cause of death, domestic dogs killed 12 of 26 deer, and coyotes killed 3. Predator species occasionally reported in the area include mountain lions, bobcats (*Lynx rufus*), and wolves (*Canis lupus*), but sightings are rare.

1.2.4.1 Body condition

Mule deer metabolic rates exhibit an annual cycle corresponding to forage availability. Summer intake of high quality forage results in mass gains followed by declines during the winter (Bandy et al. 1970). After 18 months of age, males and females show differences in seasonal body fat as a result of variation in energetic demands. Loss of body fat is most pronounced in males, and their reserves are lowest following rut and into the winter and spring; for females, the low point is following gestation and lactation (Anderson et al. 1972). During the winter, deer in northern climates reduce their metabolic rate, restrict food intake and activity, and favor environments suitable to energy conservation. Energetic deficits may result in die-offs during the winter, but stores of energy depend on nutritional needs being met on the annual range (Mackie et al. 2003).

In arid environments, precipitation is a key factor in forage quality and droughts can result in population decline (Lawrence et al. 2004). Bender et al. (2007a) related body condition, body fat, and precipitation to survival of female mule deer in New Mexico. Body condition in turn can affect fawn recruitment rates (Wood et al. 1989). Weather patterns, forage quality, and body condition are crucially interrelated factors affecting population dynamics.

1.2.4.2 Home range habitat and survival

Forage availability predicts deer body condition and is related to survival, and recent studies have assessed home range habitat selection measures in terms of survival. Alaskan black-tailed deer were found to be at varying risks of mortality depending on the type and stage of managed forest treatment they used (Farmer et al. 2006). Klaver et al. (2008) found a relationship between survival and seasonal range characteristics for white-tailed deer in South Dakota and Wyoming. Survival was highest in ranges with higher proportions of large trees and with lower proportions of grasses and forbs. Mule deer fawns in Idaho were at greater risk to predation by coyotes on steep slopes, whereas fawns killed by mountain lions were in areas of greater cover or structure (Bishop et al. 2005). Caribou mortality through predation was related to use of forested areas, whereas lowland areas (peatland bogs and fens) provided some protection from predators (McLoughlin et al. 2005).

Mule deer require rugged terrain and shrubland for cover; grass and shrubland for forage; and wetlands for forage, cover and water requirements. We tested whether the home range proportions of these habitats influenced survival.

1.2.4.3 Radio collar effects on survival

Wildlife research often involves animal handling and marking, which may affect the animal's survival, behavior, and breeding success. An assumption of survival analyses is that radio transmitters do not affect survival (Winterstein et al. 2001). Fawns with radio collars were previously suspected to be at a higher risk of predation, but at least one study found that fawns with lightweight, inconspicuous ear-tag transmitters were equally at risk (Garrott et al. 1985). Côté et al. (1998) found that capture negatively affected reproduction and caused kid abandonment by 3 and 4-year-old mountain goats in Alberta, and found that kids with radio collars had poorer survival than uncollared kids, although the effect was not statistically

significant. Radio collars negatively affected survival of juvenile San Joaquin kit foxes, particularly when they were no longer under maternal care during dispersal periods (Cypher 1997). The ratio of collar mass to body mass is usually used as a guideline when selecting collars (White and Garrott 1990) and the Canadian Council on Animal Care (2003) recommends 5% as a limit. We tested whether exceeding a limit of 2% affected survival.

1.3 Objectives

1. To estimate long distance movements of collared deer in Southern Saskatchewan including rates and orientation, and build some predictive ability, and to assess the potential of these movements to increase the geographic range of CWD.

2. To estimate probability of mule deer survival in southern Saskatchewan and estimate the role of potential factors on survival. Factors were divided into intrinsic and extrinsic measures, including body measures and condition, and home range features. The impact of radio collar on survival is also addressed.

This thesis is organized into chapters resembling journal articles. Chapter 2 addresses the first objective and chapter 3 the second objective. Chapter 4 is a thesis synthesis.

CHAPTER 2
DISPERSAL AND MIGRATION OF WILD DEER IN A CWD-ENDEMIC AREA OF SOUTHERN SASKATCHEWAN

2.1 Abstract

Chronic wasting disease (CWD) is endemic in mule deer (*Odocoileus hemionus*) of southern Saskatchewan near the South Saskatchewan (S.S.) River. Exchange of, or contact between, individuals from endemic areas and naïve subgroups of deer via dispersal or migration are potential methods of CWD spread. The ability to predict the likelihood and direction of long distance movements by mule deer from endemic areas will be valuable for disease management. We radio-collared and tracked 145 mule deer and 19 white-tailed deer from 2006–2009 to characterize their movement patterns. Results indicated adult migration and juvenile dispersal distances were similar. Male and female migration distances were also similar. Deer from a study area of vast grassland were more likely to migrate than deer in study areas fragmented by agricultural land. Proximity to grassland and high terrain ruggedness values were predictors of long distance movement paths. Migration and dispersal movements were predicted by terrain and grassland habitat associated with the S.S. River but mean migration orientation was not predicted by the S.S. River; rather, it was aligned with the expanse of grassland and hilly terrain of the Missouri Coteau north of the S.S. River. Observations of white-tailed deer (*Odocoileus virginianus*) movements in Saskatchewan and implications for CWD distribution are briefly discussed. Deer migration and dispersal patterns can be used in conjunction with home range, contact, and CWD transmission information to predict CWD spread across local landscapes.

2.2 Introduction

Chronic wasting disease (CWD), a cervid-specific transmissible spongiform encephalopathy (TSE), was first detected in a wild mule deer (*Odocoileus hemionus*) in Saskatchewan, Canada, in 2000. The provincial Ministry of Environment (MOE) promptly organized a herd reduction program to reduce deer density and thereby decrease disease transmission. Increased hunter opportunities were provided in select wildlife management zones where CWD had been detected. Herd reduction failed to eradicate CWD from the wild, and its prevalence and geographic extent have steadily increased over the past ten years (CCWHC, unpublished data).

Chronic wasting disease has multiple routes of transmission and continues to spread in wild cervid populations, resulting in a challenging management scenario. Transmission can occur by contact with infected deer or prion-contaminated environmental sources (Mathiason et al. 2009). Infected deer shed prions in bodily fluids (Mathiason et al. 2006) and carcasses are also sources of infection (Miller et al. 2004). Prions remain infective in the environment for periods of years (Johnson et al. 2006, Wiggins 2009), further complicating CWD management.

Host movement patterns likely play a role in wildlife disease spread (Miller et al. 2000). CWD prevalence is heterogeneous in landscapes where it is found, and is probably influenced by wild deer distribution and movements (Conner and Miller 2004). Recently, Silbernagel (2010) identified factors affecting mule deer home range size in this area of Saskatchewan. Male home ranges were larger than female home ranges, and terrain ruggedness, Shannon's diversity of habitat, study site, number of habitat patches, and proportion of cropland all influenced home range size. Large-scale movements, including dispersal and migration, also affect disease expansion through time and space in wild cervid populations (Conner et al. 2008). There have been no previous studies of long distance movements by mule deer in Saskatchewan.

Deer movements outside the home range can be long distances during certain life stages. Dispersal movements are most often by young males and sometimes by young females (Robinette 1966, Hawkins and Klimstra 1970), whereas dispersal movements by adults are less common (Wood et al. 1989). Migration is an adaptation to seasonal changes in energetic demands and resource availability. In mountainous regions, mule deer migrate to take advantage of quality forage at higher elevations in summer and take cover at lower elevations in winter (Garrott et al. 1987). Mule deer are generally non-migratory in the prairies (Mackie et al. 2003), but previous studies have documented mixed strategies (Nicholson et al. 1997). Seasonal migration results in varied deer density and association rates—deer typically congregate in winter yards where they contact each other or share habitat more frequently (Conner et al. 2008, Silbernagel 2010). Thus, migration may influence disease transmission rates whereas dispersal is thought to affect disease spread to new areas (Conner et al. 2008). Even short-term movements outside the home range have potential to transmit disease (Skuldt et al. 2008).

Mule deer studies in the Canadian prairies are scarce and disease management decisions have been made without scientific knowledge of local deer movement behavior. We attempted to fill this knowledge gap by radio-collaring and tracking wild deer in a CWD-endemic area. Our objective was to estimate distance of movements by radio-collared mule deer in Southern Saskatchewan by determining rates and orientations of dispersal, migratory, and excursion movements. We examined landscape factors associated with long distance movements, and assessed the potential of these movements to further increase the geographic range of CWD in Saskatchewan.

2.3 Methods

2.3.1 Study Area

The study was conducted along the South Saskatchewan River basin in the Prairie Ecozone of southern Saskatchewan, Canada. The landscape was dominated by relatively flat low-lying terrain interrupted by areas of kettle topography including river valleys and coulees, sand hills, and rolling terrain.

The total study area size was 2740 km^2 and included 5 study sites: Antelope Creek (ANT; 248 km^2; 50.66°N, 108.27°W at center), Beechy pasture (BEE; 613 km^2; 50.98°N, 107.70°W), Douglas park (DOU; 605 km^2; 51.02°N, 106.44°W), Matador pasture (MAT; 810 km^2; 50.77°N, 107.73°W), and Swift Current Creek (SWI; 464 km^2; 50.58°N, 107.73°W). See Figure 2.1.

The study areas were within two prairie ecoregions: Mixed Grassland and Moist Mixed Grassland. Short grasses in the area were blue grama (*Bouteloua gracilis*) and sedge (*Carex* spp.) and mid-to-tall grasses included wheatgrasses (*Agropyron* spp.), Junegrass (*Koelaria macrantha*), needle-and-thread (*Stipa comata*), and western porcupine (*Stipa spartea v. curtiseta*). Pasture sage (*Artemisia frigida*) and moss phlox (*Phlox hoodii*) were common forbs; common shrubs included Western snowberry (*Symphoricarpos occidentalis*), wolf willow (*Eleagnus commutata*), creeping juniper (*Juniperus horizontalis*), chokecherry (*Prunus virginiana*) and Saskatoon berry (*Amelanchier alnifolia*) (Acton et al. 1998). Trees were uncommon except in the DOU site, where the dominant species were trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*). Common crop types in the grassland region of Saskatchewan included wheat, barley, oats, canola, mustard, peas, lentils, and flax (Government of Saskatchewan 2009).

Saskatchewan has long, cold winters and short, warm summers. Average temperature in the south during the coldest month of winter (January) was -13°C and in the warmest month of

summer (July) was 19°C. Mean annual precipitation was 414 mm (Canadian Plains Research Center 2006).

The total area and proportions of grassland and cropland varied between sites (Figure 2.2). ANT and SWI sites were dominated by agricultural land (Figure 2.3) parceled by the public land survey system with regular grid roads every 2 by 1 mile. Core areas of deer use existed in the rugged grassland terrain along the S.S. River or its drainage streams. DOU was named after Douglas Provincial Park in the core of its study area; deer within park boundaries were afforded protection from hunting pressure which helped maintain high deer densities. DOU, BEE, and MAT sites were characterized by large expanses of hilly native pasture with agricultural areas at the periphery. These areas had sparse human habitation and few roads. All areas except BEE were adjacent to the S. S. River which was dammed near the DOU site forming Lake Diefenbaker. Although BEE and MAT sites were considered independent at the beginning of the study, early observations indicated many deer moved seasonally between the two sites and for analyses we considered them as one study site (hereafter referred to as BEEMAT).

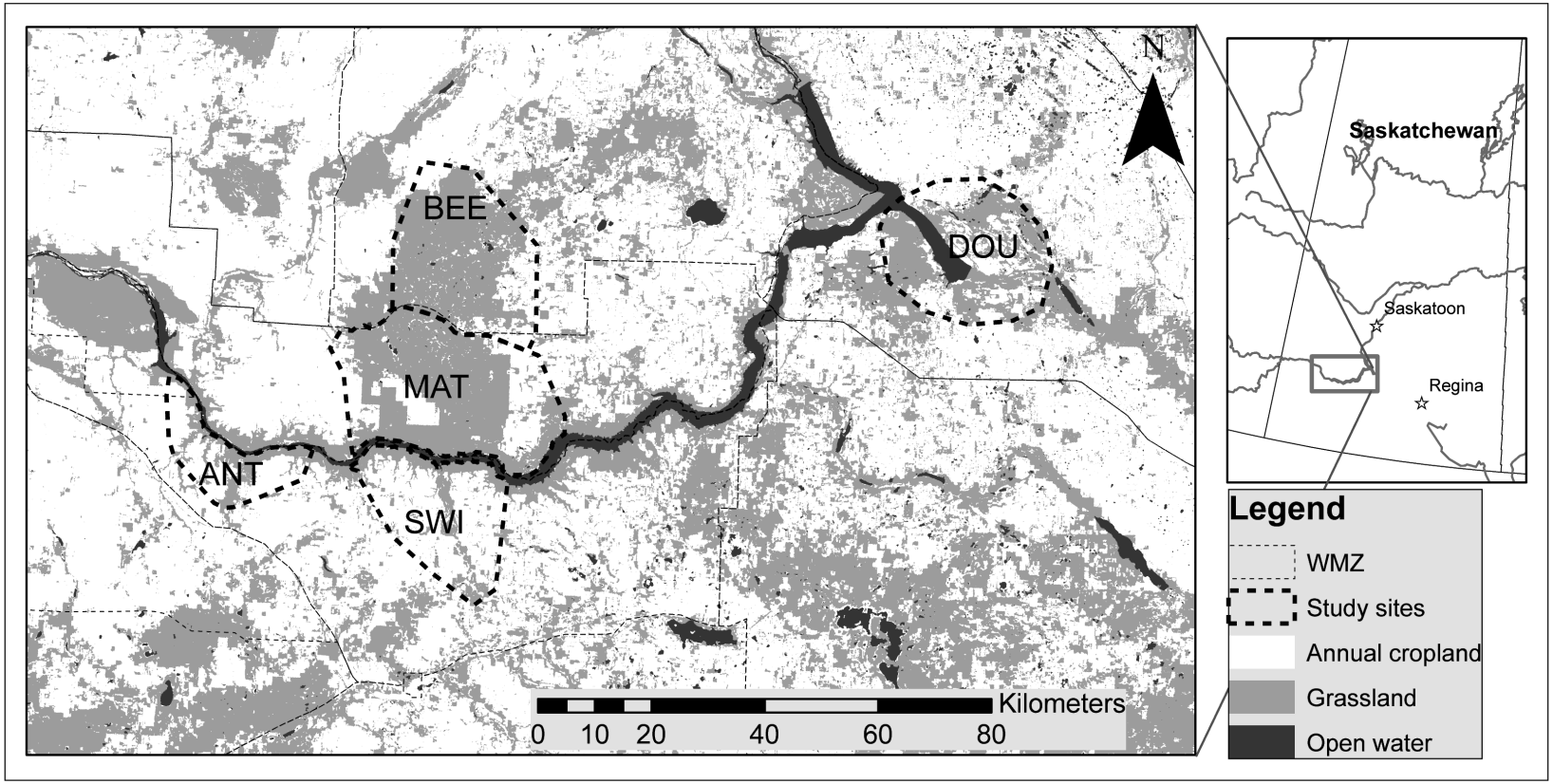

Figure 2.1: Map of study sites in southern Saskatchewan along the South Saskatchewan River. WMZ are wildlife management zones.

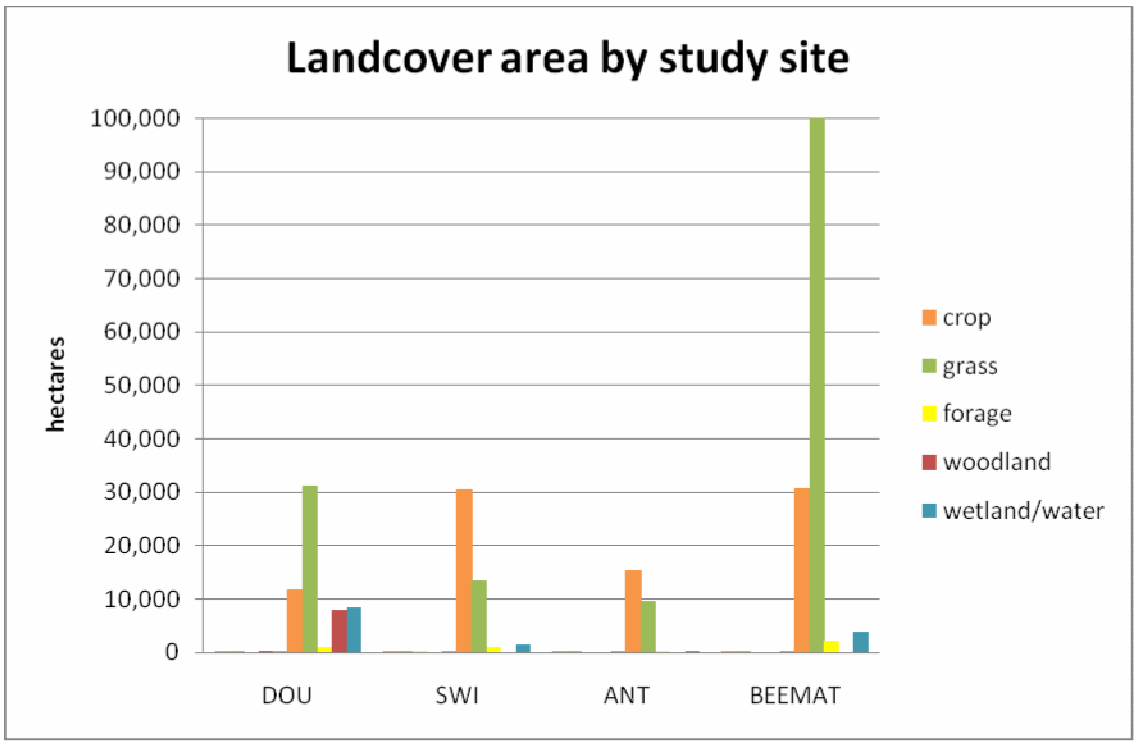

Figure 2.2: Total landcover area for each study site.

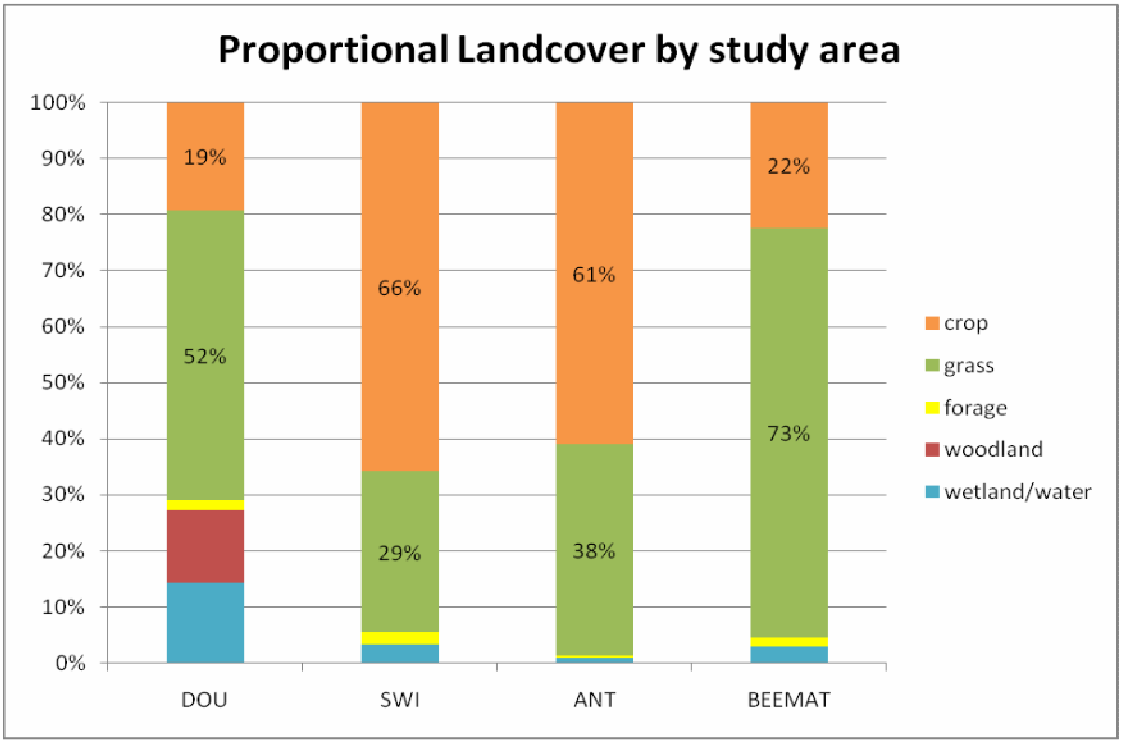

Figure 2.3: Proportional landcover for each study site.

CWD has been found in wild deer in all study areas except DOU. Population reduction programs to manage CWD began in SWI in 2002, expanded to include ANT, and MAT the following year, and in 2007 expanded to include BEE. White-tailed and mule deer ranges overlap in Saskatchewan and both species were found in the study areas. Mule deer were more common and had a higher prevalence of CWD. Figure 2.4 shows the distribution of the total number of CWD-positive wild deer detected in the province (Saskatchewan Ministry of Environment 2010). The study site was centered on the area north of Swift Current (Figure 2.5).

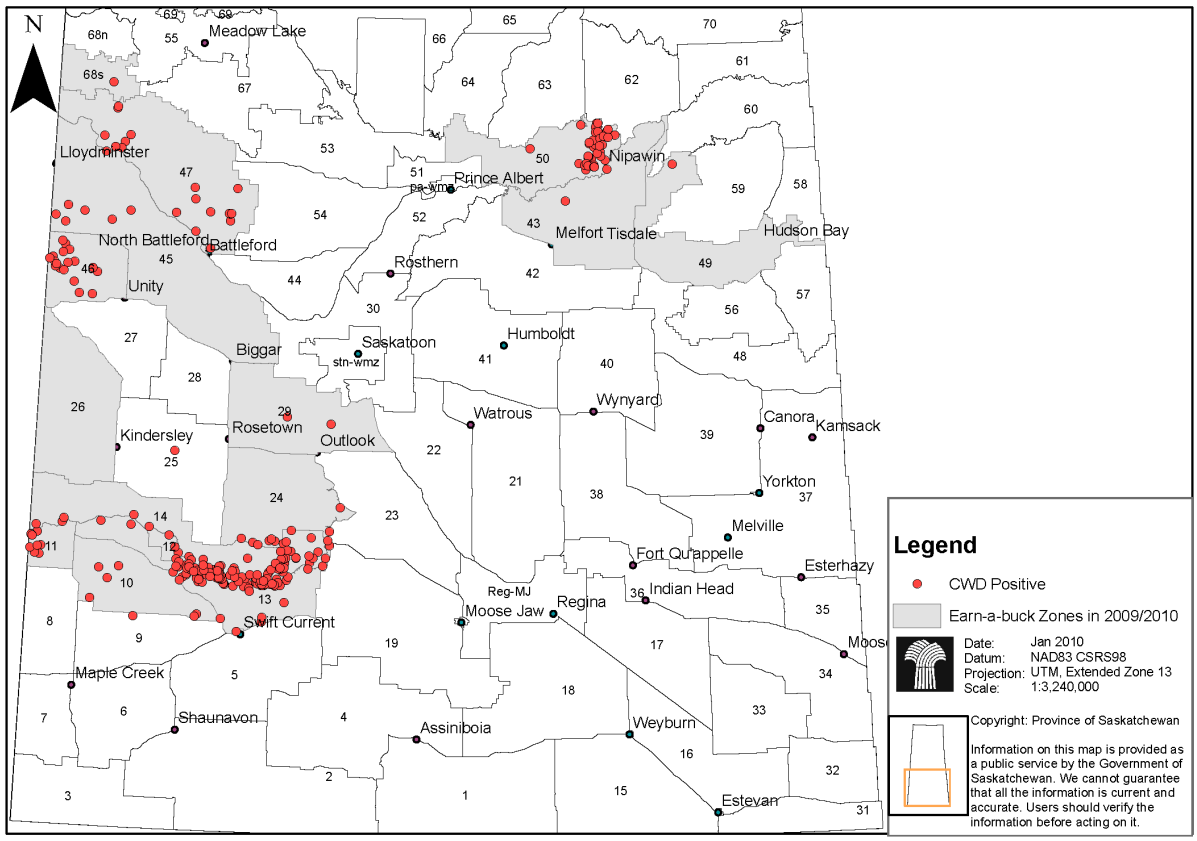

Figure 2.4: Locations of CWD positive wild deer in Saskatchewan, updated January 14, 2010. Numbers indicate wildlife management zones.

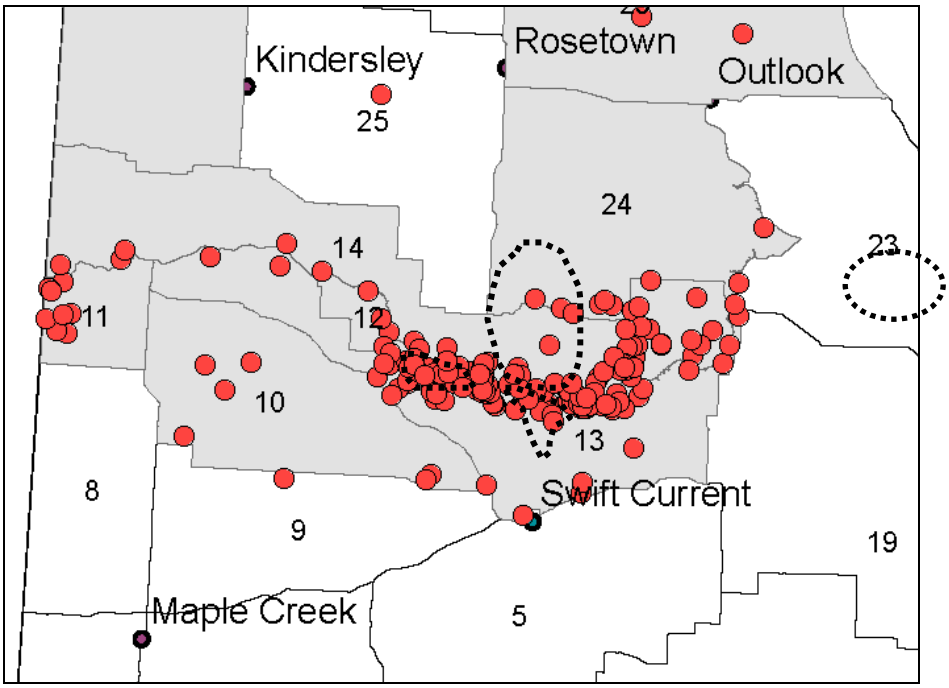

Figure 2.5: Inset of previous map showing study area (dashed lines). Numbers indicate wildlife management zones.

2.3.2 Capture

Between April 2006 and April 2008, mule and white-tailed deer were captured by helicopter net-gunning (Bighorn Helicopters Inc., Cranbrook B.C.) (Krausman et al. 1985) and Clover traps (Clover 1956). Deer caught in traps were anaesthetized immediately after technicians approached and collapsed the trap, and once anaesthetized, blindfolds and hobbles were applied. Deer transported by helicopter were blindfolded and hobbled prior to anaesthetization. Each deer was anaesthetized using Xylazine-Telazol (Rompun®; Telazol®) in order to test for CWD on tonsil biopsy (Schuler et al. 2005), and later reversed with Atipamezole (Antisedan®). Age was assessed by body size and tooth wear (Severinghaus 1949, Robinette et al. 1957). Deer aged 6 to 10 months old at capture were classed as juveniles; between 1–2 years as yearlings; and over 2 years as adults. Individuals were ear-tagged with a numbered plastic cattle tag color-coded to study site, and a small metal numbered ear-tag (Ketchum Manufacturing

Inc., Brockville ON K6V 7N5, Canada). Radio collars were Lotek GPS 3300 or 4400 or VHF (Lotek Wireless Inc., Newmarket ON L3Y 7B5, Canada) or expandable VHF (Advanced Telemetry Systems, Isanti, MN 55040, USA). Capture protocol was approved by the University of Saskatchewan Animal Care Committee (20050135).

In 2008 we attempted to reduce collar loss from slippage on juveniles. Males were collared with expandable VHF and females with fixed-circumference VHF and a sample (n = 4; 1F, 3M) were collared with a lightweight (300 g) GPS transmitter (Televilt by Followit Holdings AB, Lindesberg, Sweden). The latter group's collars failed prematurely. In all capture years, all non-expandable male collars were fitted with a nylon-enveloped foam insert to allow for neck expansion during the rut. Collars had mortality sensors activated by a period of immobility (6 to 12 hours, depending on the collar type).

GPS collars were set to collect locations every 4 hours, or every hour during breeding and fawning seasons, and also recorded altitude and temperature. Minimum monthly locations (VHF) or signal checks (GPS) were acquired via fixed-wing aircraft telemetry (Mech 1983) or on the ground by hand-held antenna telemetry. Location accuracy for VHF collars, estimated from known collar locations, was 678 m (SE = 48, n = 82). GPS collar accuracy was reported by LOTEK at 5 m. We evaluated their accuracy at 11.3 m (SE = 2.6, n = 4). To assess accuracy, we calculated the mean x and y positions of stationary collar data and then calculated the average distance of all fix locations from the mean. Data were plotted in UTM coordinates for all analyses.

2.3.3 Definition and Measurement of Long Distance Movements

Dispersal was defined as a permanent movement from an animal's natal range to a new, non-overlapping range. Dispersal is usually undertaken by juvenile males, between 6 and 24 months of age, but has been reported in all age-sex classes (Robinette 1966, Holzenbein and

Marchinton 1992, Nelson and Mech 1992, Kenward et al. 2001, Nixon et al. 2007). Since the natal range of only the former group is known, only they were included in dispersal observations. Migration was defined as movement between non-overlapping seasonal ranges (Brown 1992, Brinkman et al. 2005, Sawyer et al. 2005). Obligatory migrants moved to winter range in early winter where they resided until spring (Sabine et al. 2002), whereas conditional migrants failed to migrate during one season or migrated unpredictably (Nelson 1995, Brinkman et al. 2005). Resident deer had one home range area year-round and never migrated (Vercauteren and Hygnstrom 1998). Short-term movements outside the normal home range area (i.e., <1 month) were termed "excursions," as long as the deer returned to its normal range. These were observed for all categories of deer.

Home range polygons were calculated as 95% kernel density estimates (KDE) (Rodgers et al. 2007) in ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, Calif.). Least squares cross validation (LSCV) is recommended for smoothing factor (h) selection in KDE; however, LSCV methods will generally fail at sample sizes > 100 or < 10 (Hemson et al. 2005). We used LSCV methods for VHF-collared deer with suitable sample sizes. GPS-collared individuals had sample sizes > 100 and for these 275 m was selected as a smoothing factor because h*ref* (software-generated reference bandwidth) tends to over-smooth and inflate home range size (Seaman et al. 1999). The goal was to delineate separate ranges objectively. Home range size was not evaluated in this study.

The centroid of each range polygon was calculated (ET SpatialTechniques, Pretoria, South Africa) and used to measure movement orientation and distances between seasonal or natal and adult ranges (Kernohan et al. 1994, Zar 1999). For seasonal ranges, we measured the travel orientation from winter range to summer range. For excursions and atypical migrations,

we measured the travel orientation from the dominant range (where it ranged the majority of its time) to the short-term range. For dispersing deer, we measured the orientation from natal range to adult range. Distances between centroids <5 km were not considered long distance movements. Date of movement was recorded as the first location outside of the previous range, or the first date the individual was not located in its usual range if it was subsequently located in a new range. GPS data were accurate to the day and VHF data were accurate to the month.

We removed deer from analyses if their research lifespan was shorter than 6 months due to collar loss, collar failure, or death. Exceptions were made for 2 juvenile deer that died within 6 months of capture but had clearly dispersed. We excluded resident deer studied less than a year from analyses because they had potential to migrate but died. We classified migratory deer studied for 18 months or longer as conditional or obligatory.

2.3.4 Dispersal Rate

Since dispersal rate calculated as the number of dispersals per juvenile captured would be inaccurate due to death loss and new captures varying the number of juveniles available at each dispersal period, we estimated annual dispersal rate for each cohort using an adaptation of Kaplan-Meier survival model (Holzenbein and Marchinton 1992, Kaplan and Meier 1958, Pollock et al. 1989, Long 2006). In a survival model, deaths reduce the population survival rate, whereas in this model, dispersals reduce the philopatry rate. Dispersal rate is simply one minus the philopatry rate. Rates were calculated over monthly intervals and mortalities were censored from the number of individuals available to disperse.

2.3.5 Factors Associated with Long Distance Movements

The movement paths of a subset of GPS-collared mule deer (n = 33) that migrated or dispersed were analyzed to determine features associated with locations along the chosen travel

path between home ranges. These features may describe habitat preferences of travelling mule deer and can be used to predict deer movement and future disease spread.

We used the last location in the home range, first location in the new home range, and all locations between to represent the chosen travel path. A minimum of 3 GPS positions (collected in 1, 4, or 6-hour intervals) was used to create a digitized line representing the travel path. Using alternate animal movement routes tool (Jenness 2005) in ArcView® GIS 3.2 (Environmental Systems Research Institute, Redlands, Calif.), ten lines of equal length and shape were randomly generated from the point of origin for each deer's path (Long 2006) to represent alternatives to the selected path. Vertices of all lines were used as sample points (n = 4796) to measure landscape attributes (Bruggeman et al. 2007) including habitat (land cover type, patch size and patch area–perimeter ratio), topography (TRI and elevation), and proximity to landscape features (river, wetland or open water, paved or grid roads, grassland and cropland). Because the point of origin was equivalent for chosen and random lines, it was removed from analysis.

A 56m-resolution 2006 land cover map was acquired from the Agricultural Financial Services Corporation (AFSC; Lacombe, AB; T4L 1B1). We simplified the 9-class cover map into 7 classes: annual cropland, grassland (pasture), forage (hay), forest, wetland, water, and other (built-up, barren, or unclassified). Shrubland was not a class in the cover map but most grassland in the study area is native and partly shrub-covered. Digital elevation model data were transformed into a terrain ruggedness index (TRI) (Russell and Levitin 1995). Proximity to landscape features was calculated with the near tool in ArcInfo 9.3 (Environmental Systems Research Institute, Redlands, Calif.).

2.3.6 Statistical Analyses

Statistics on migration were calculated using only adult deer and dispersal using only deer captured as juveniles. Data distributions for each category of movement were tested for

normality. Data distributions tested normal (1-sample KS test: excursions, $P = 0.32$; migrations, $P = 0.077$; dispersals, $P = 0.087$), but migration and dispersal distances were tested with non-parametric methods because they were approximately non-parametric (Figure 2.6). For migrations and dispersals, differences in movement distances between sexes were evaluated with a Mann-Whitney *U* test, and for study sites a chi-square test. For excursions, we used *t*-tests for differences between sexes and one-way ANOVA for study site differences. The low sample size of dispersals prevented statistical comparisons between sexes. All statistical analyses were performed with SPSS software (version 17.0; SPSS Inc., Chicago, Ill.).

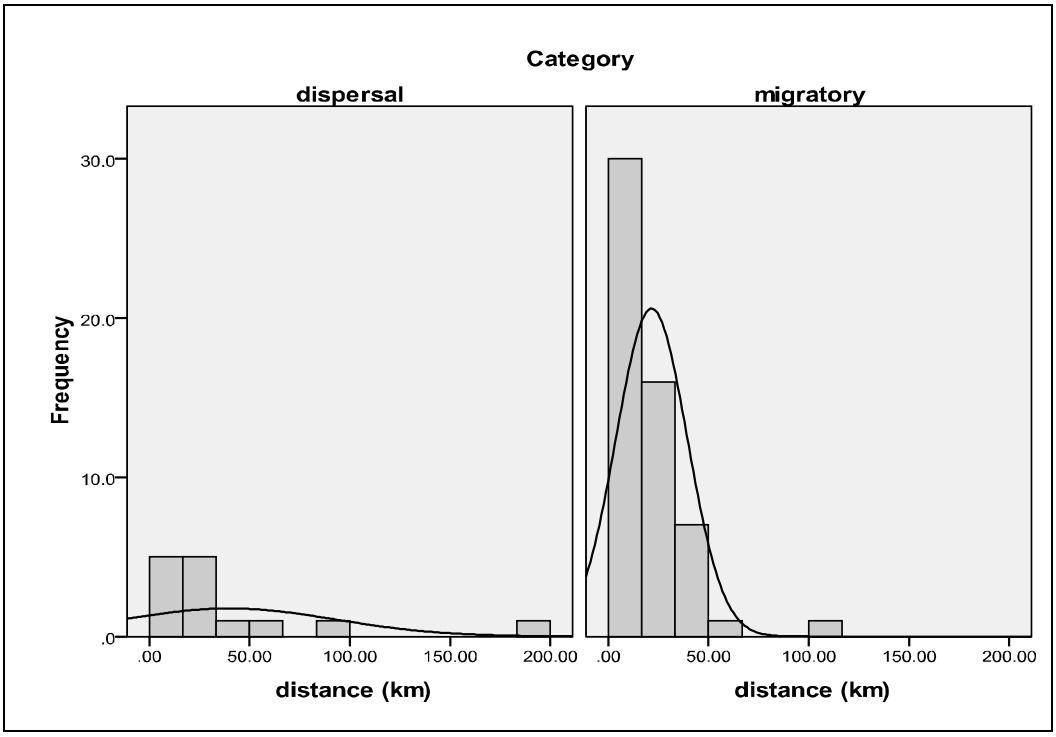

Figure 2.6: Frequency histograms of dispersal distance (left) and migration distance (right).

Directional analyses of migration and excursion datasets were completed using Oriana software (Kovach Computing Services©). For data independence, we selected one migration per deer (winter to summer) and randomly selected one excursion per deer. Two circular distribution tests assessed directionality: Rayleigh's uniformity test and Rao's spacing test.

Rayleigh's uniformity test detected normal distribution of directions around a circle, and if the null hypothesis was rejected, then it was most likely that a direction was preferred. Rao's spacing test also assessed normality of directions, where the null hypothesis was that deer movement directions were random and distributed uniformly about a circular compass (0 to 360°). Rao's test was considered a stronger test because it assessed whether the distribution was evenly spaced, i.e., spacing between points should be approximately 360°/n. The latter test detected clusters of directionality whereas Rayleigh's might not (Kovach 2009).

The landscape features associated with chosen paths for long distance movements were assessed using generalized estimating equations (GEE) with an exchangeable correlation matrix, binomial distribution, and logit link function. Data were clustered by individual deer as subjects, and further clustered within each subject by unique path and sequential location along path. Variables that scored $P < 0.2$ in simple regression analyses were included in multiple regression models. Backward removal of variables was then performed with significance for model inclusion set at $\alpha \leq 0.05$. Because GEE are non-likelihood based, QIC (quasi-likelihood under independence model criterion) was recommended over AIC for GEE model selection (Pan 2001). QIC values were assessed to select the correlation structure and QICC (corrected quasi-likelihood under independence criterion) values were assessed to select the best set of parameters (Garson 2009). Final model variables were tested for correlation and interaction with one another. If Spearman's r was > 0.7, one of the correlated variables was removed based on biological reasoning and/or based on significance values.

2.4 Results

2.4.1 Long Distance Movements

One hundred and sixty-four deer (145 mule, 19 white-tailed) were used to categorize movement. Of these, 4 lived less than a year but 141 were studied for a period of 1 to 3 years, and the average time in the study was 21 months. Fourteen juveniles were classified as dispersers, 55 adults as migrants, and 76 adults as residents.

2.4.1.1 Dispersal

Between spring 2007 and autumn 2008, 14 juvenile mule deer dispersed a median distance of 22.8 km (SE = 13.6; $\bar{x}$ = 39.9 km; range 6.5–195.5 km). More males (n = 10) dispersed than females (n = 4) and 11 (4 F, 7 M; 5 in 2007, 6 in 2008) dispersals were initiated in the spring around fawning time (June). Three dispersals occurred during autumn rut; all were male and all occurred in 2007. Ten deer were approximately 12 months of age at time of dispersal (7 M, 3 F), 3 were 18 months (M), and 1 was 24 months (F). Most dispersals were from ANT (n = 8), and 2 each were from the other sites (Table 2.1). Pearson's χ^2 results (1.145, df = 3, P = 0.766) showed no difference between study site in the proportion of dispersers and residents.

Table 2.1: Mule deer dispersal details

deer_id	site	dispersal distance (km)	bearing (°N)	season	age (months)	sex	Dispersal initiation date	capture date
O016	ANT	54.7	101	spring	12	F	18-May-07	13-Mar-07
Y024	BEEMAT	17.5	19	spring	12	M	29-May-07	12-Mar-07
B028	DOU	98.9	27	spring	13	F	05-Jul-07*	16-Mar-07
O022	ANT	33.6	99	spring	13	M	05-Jul-07*	13-Mar-07
O050	ANT	25.0	320	spring	13	F	05-Jul-07*	09-May-07
O010	ANT	6.5	105	autumn	17	M	01-Nov-07	13-Mar-07
O011	ANT	20.6	284	autumn	17	M	06-Nov-07*	13-Mar-07
P049	SWI	8.4	105	autumn	18	M	06-Dec-07*	14-Mar-07
Y069	BEEMAT	15.3	332	spring	11	M	06-May-08*	09-Mar-08
O057	ANT	33.2	93	spring	13	M	14-Jun-08	09-Apr-08
O053	ANT	25.0	107	spring	13	M	21-Jun-08	22-Mar-08
B027	DOU	11.3	95	spring	24	F	25-Jun-08*	16-Mar-07
P053	SWI	195.5	283	spring	13	M	25-Jun-08*	08-Mar-08
O059	ANT	13.2	335	spring	14	M	05-Aug-08*	12-Apr-08

*indicates flight date--dispersal date is approximate

We intended to compare study site dispersals by collaring an equal number and similar gender ratio of juveniles per site, but were unsuccessful due to mortality, collar losses, and difficulty finding juveniles in some areas. As a result, the number of juveniles studied at each site was unequal (Table 2.2). Nevertheless, we have reported the results from a study site context. Juvenile mule deer included in analyses for each site were 15 (ANT), 9 (BEEMAT), 12 (DOU), and 8 (SWI). ANT had a higher number of juvenile males collared than any other site. Numbers of juveniles available (alive and had not dispersed previously) per dispersal period averaged over the 4 seasonal dispersal opportunities were 5.7 (ANT), 3.6 (BEEMAT), 4.2 (DOU), 4.5 (SWI). In June 2007 there were 10 juveniles available at ANT, compared to 4, 5, and 6 respectively at BEEMAT, DOU, and SWI. This was the first potential dispersal period of the study and also had the highest contrast in number available per site.

Table 2.2: Summary of juveniles and dispersal movements by study site.

	ANT	BEEMAT	DOU	SWI	ALL
Captured juveniles (JUV)	15	9	12	8	44
male	9	5	4	4	22
female	6	4	8	4	22
Average # JUV available	5.7	3.6	4.2	4.5	4.5
male	2.3	0.5	2.0	2.0	1.7
female	3.5	3.2	2.2	2.5	2.8
Dispersal count	8	2	2	2	14
male	6	2	-	2	10
female	2	-	2	-	4
Avg. dispersal distance (km)	26.5	16.4	55.1	102.0	39.9
male	22.0	16.4	-	102.0	36.9
female	39.8	-	55.1	-	47.5

Using the dispersal rate adapted from Kaplan-Meier, the dispersal rate from capture in late winter until year-end for the 2007 cohort was 0.36 (±0.21), and for the 2008 cohort was 0.65 (±0.32) (Figure 2.7). The overall dispersal rate from spring 2007 through autumn 2008 with both cohorts was 0.55 (±0.17) (Figure 2.8). There were no dispersal events in autumn 2008, the last dispersal period studied.

The farthest dispersal distance of 195 km was between capture at Swift Current Creek and mortality location in southeastern Alberta along the South Saskatchewan River. Dispersing deer from ANT and SWI tended to travel with the orientation of the river, as seen in Figure 2.9. Two dispersers from ANT settled in SWI (O016 and O057) and another (O016) dispersed to SWI but died during settlement 2 weeks after leaving its natal range. One juvenile white-tailed dispersed—a male from SWI that moved 36 km to ANT at 12 months of age and was dead where it was found.

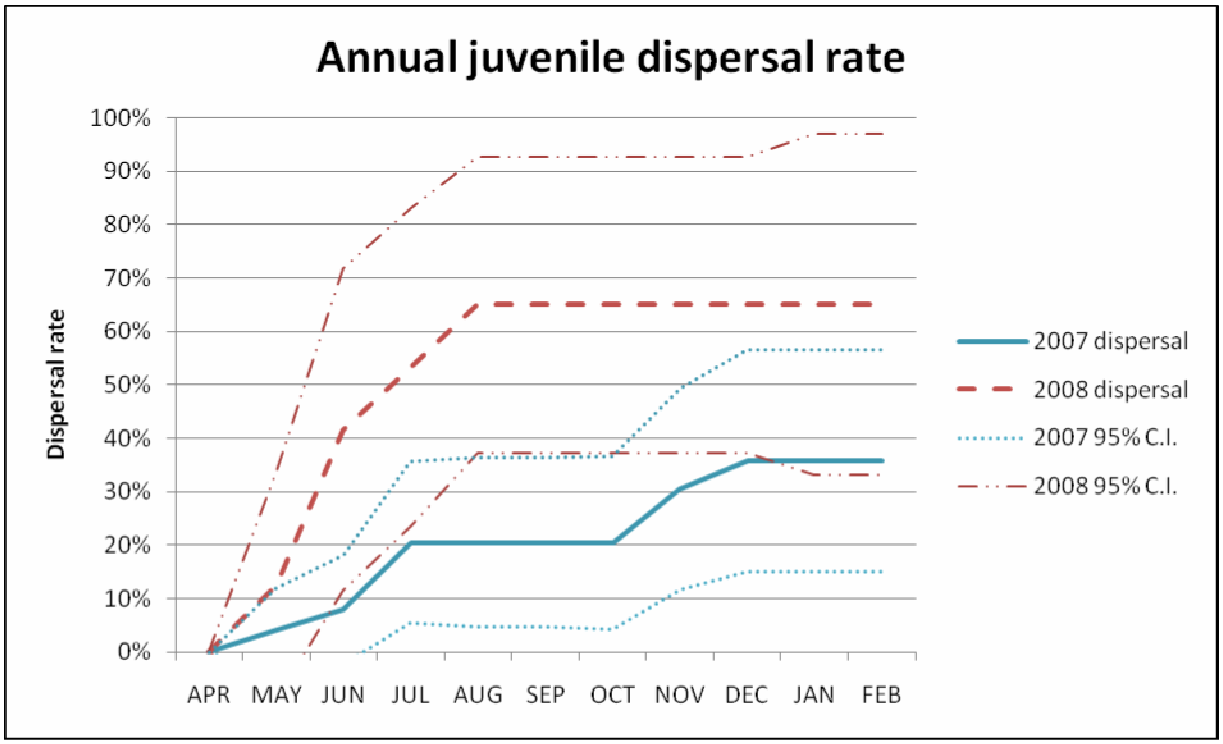

Figure 2.7: Annual juvenile dispersal rate for 2007 and 2008 cohorts.

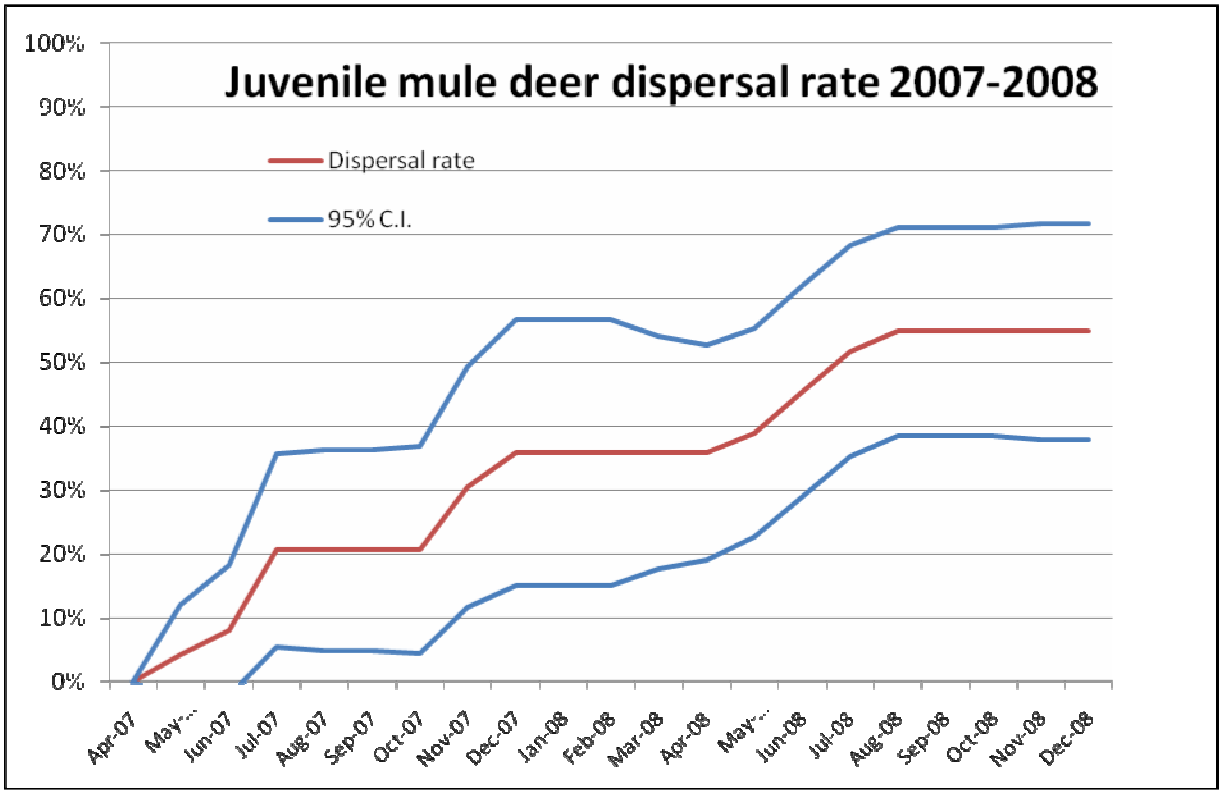

Figure 2.8 Overall juvenile dispersal rate 2007–2008. Confidence intervals vary through time depending on the number of juveniles alive in the study, narrowing with additional captures and widening with losses.

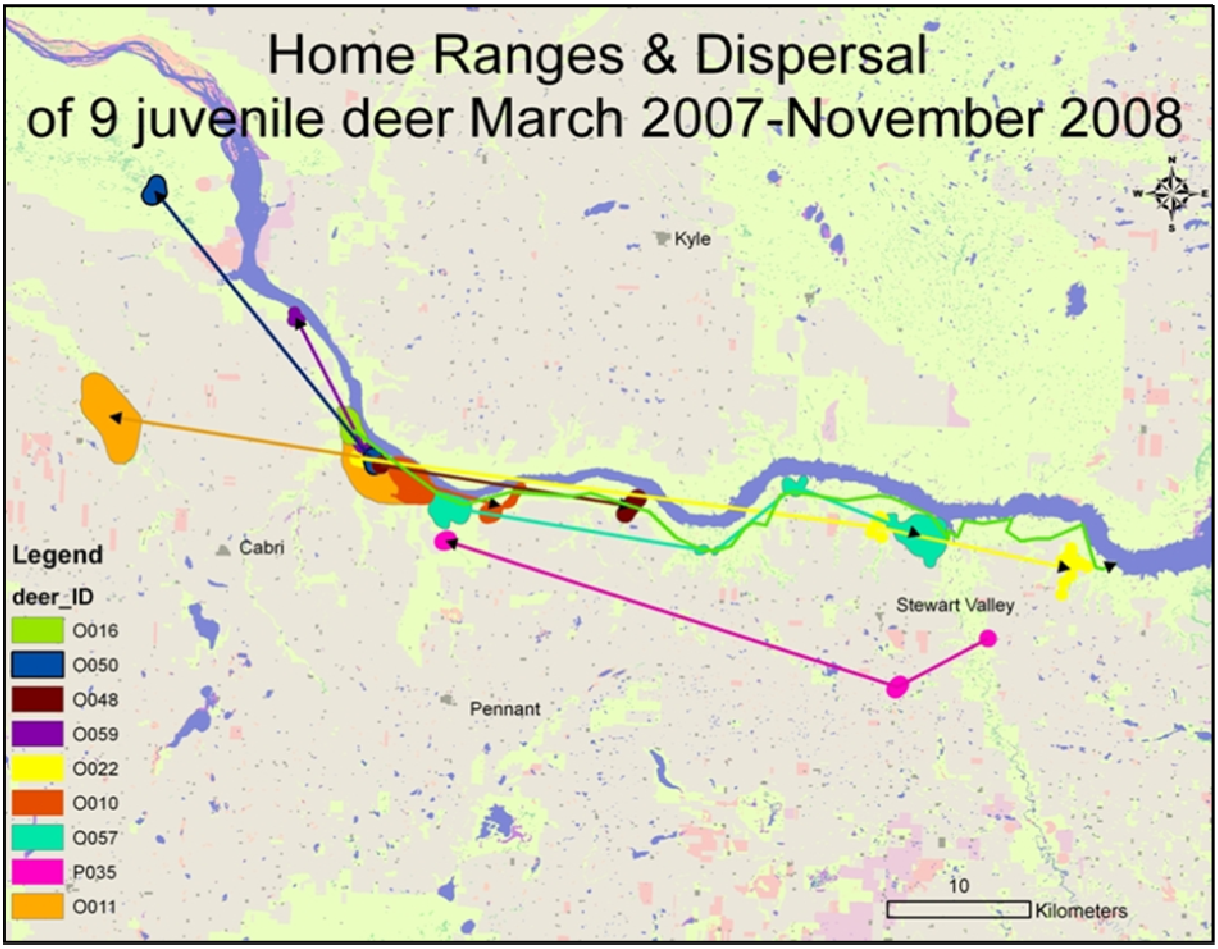

Figure 2.9: Juvenile dispersals from the ANT site and 1 from SWI to ANT. All are mule deer except P035, a white-tailed deer from SWI.

2.4.1.2 Migration

Median migration distance of adult mule deer was 16.0 km (SE = 2.6, $\bar{x}$ = 22.8 km) and ranged from 5.0 to 112.6 km. Forty-two per cent of adults were migratory (n = 49) and 58% were resident (n = 67). Most of the migratory deer were from the BEEMAT site, where 68% of adults migrated compared to 24 to 30% at other sites (Table 2.3). The proportion of migratory deer per study site differed significantly (χ_3^2 = 19.533, $P \leq 0.001$). However, relative proportions could have been inflated because deer that behaved as residents but lived less than 1 year (n = 6) were removed from analyses, whereas deer that migrated and lived between 6–11 months were

included (n = 13). Migration distances were not equivalent between study sites (χ_3^2 = 9.392, P = 0.025). Tested pair-wise, we found significant differences between BEEMAT and DOU (Z_1 = -2.105, P = 0.039) and BEEMAT and SWI (Z_1 = -3.040, P = 0.002).

Thirty-nine per cent of males and 45% of females were migratory (Table 2.3). Median migration distance was similar for both sexes (Table 2.4) (Z_1 = -0.357, P = 0.721).

Table 2.3: Number and proportion of migratory and resident adult mule deer, by study site and by sex.

ADULT MULE		migratory		resident		Total
		n	%	*n*	%	*n*
SITE	ANT	6	24%	19	76%	25
	BEEMAT	30	68%	14	32%	44
	DOU	5	25%	15	75%	20
	SWI	8	30%	19	70%	27
SEX	F	29	45%	36	55%	65
	M	20	39%	31	61%	51
Total		49	42%	67	58%	116

Table 2.4: Adult mule deer migration distance by study site and by sex.

ADULT MULE		distance (km)					
		median	SE	$\bar{x}$	Min	max	*n*
SITE	ANT	16.0	4.9	18.3	5.6	37.6	6
	BEEMAT	25.8	1.9	24.2	8.1	48.4	30
	DOU	12.5	1.7	11.2	6.0	15.6	5
	SWI	8.9	14.0	28.2	5.0	112.6	8
SEX	F	19.7	3.7	23.5	5.6	112.6	29
	M	15.7	3.5	21.7	5.0	65.4	20

Of 29 migratory deer studied a minimum of 18 months, 16 (55%) were conditional and 13 (45%) were obligate migrants. The latter category included 8 from BEEMAT, 2 from DOU, and 3 from SWI. The gender ratio of conditional migrants was similar (7 F, 9 M), whereas obligatory migrants were most often female (10 F, 3 M). Median migration distance was similar between obligatory (16.0 km) and conditional (14.7 km) migrants (Z_1 = 0.219, P = 0.846).

At least one repeat movement did not fit into our description of obligate migration. A male from DOU made a 25 km migration for approximately 1 month (August) in 2 consecutive years: this short-term movement did not fit into the regular seasonal pattern so was not considered obligate.

2.4.1.3 Dispersal vs. migration

Mule deer migration distances were similar to dispersal distances (Z_1 = -1.134, P = 0.26). Five movements by adult deer fit the description of dispersal but were more appropriately classed as conditional migrations because their natal ranges were unknown. They were marked by a long distance movement preceded by annual residence in an established range or followed by residence in the new range for at least 2 seasons. The longest distance of an adult conditional migrant was that of a 3-year-old GPS-collared mule doe (P012) that was captured February 2007 in the SWI study site. She held a home range in the area for the next 16 months until she departed June 8, 2008 to a destination 113 km away in a south-western direction (253°). She stayed in a small home range area for approximately one month, presumably fawning, and then relocated to another range 10 km to the east until September 6, 2008. For the next month, GPS locations were sporadic but she was headed eastward and died of unknown cause October 8, 53 km east of the fawning range.

Average migration distance by white-tailed deer was 37.6 km (n = 6; SE = 8.4 km; range 9.2–79.8 km; 4 F, 2M). June 6–8, 2007 an adult white-tailed doe (B063) moved 80 km from her capture location in DOU at 3 years of age. Her destination to the northeast was similar to that of a female mule deer that dispersed in 2007 (B028). A year later B063 made a brief visit to her original home range from June 13 to July 1, 2009 and then returned to her new range.

2.4.1.4 Excursions

Mean excursion distance was 9.0 km (SE = 0.8, n = 56 deer). Average distance for females was 8.6 km (SE = 1.0, n = 38) and for males was 9.8 km (SE = 1.1, n = 18). Excursion distances did not differ between sexes (t_{55} = -0.745, P = 0.459) or study sites ($F_{3, 55}$ = 1.214, P > 0.3) (Table 2.5). Mean excursion distance was similar for all months ($F_{11, 55}$ = 1.059, P > 0.4) (Table 2.6 and Figure 2.10).

Table 2.5: Excursion distance (km) by study site

site	$\bar{x}$	SE	Median	Range	n
ANT	9.0	1.8	6.4	18.9	13
BEEMAT	10.4	1.2	8.9	30.1	25
DOU	7.2	1.5	6.5	12.9	10
SWI	6.8	1.7	4.2	12.5	8
Total	9.0	0.8	7.8	32.0	56

Table 2.6: Mean excursion distance (km) per month

Month	n of deer	Mean distance (km)	SE
Jan	8	10.5	3.7
Feb	3	8.5	3.4
Mar	14	9.1	1.1
Apr	10	7.1	1.6
May	6	11.5	2.0
Jun	6	11.7	2.6
Jul	3	4.4	0.2
Aug	9	6.5	0.8
Sep	3	7.0	1.5
Oct	7	6.1	0.9
Nov	16	8.0	1.3
Dec	11	9.3	1.3
Annual	96	8.5	0.5

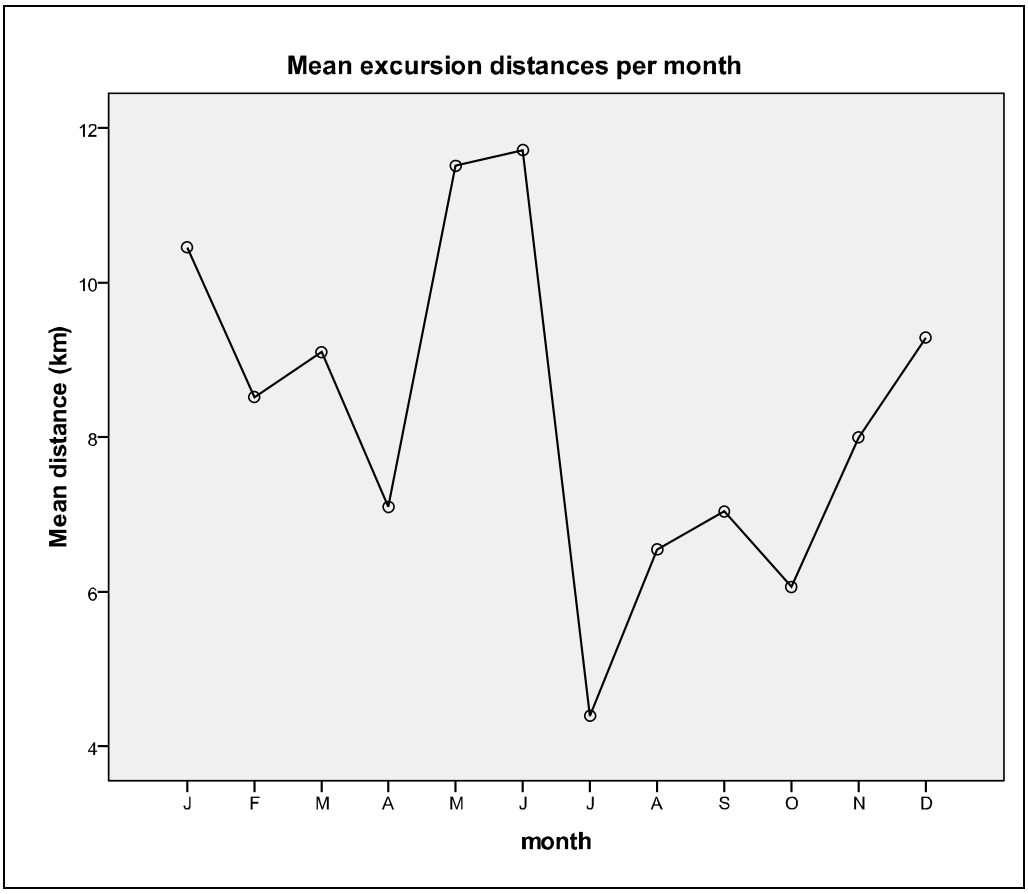

Figure 2.10: Mean excursion distance (km) per month

Excursions by males were most common during peak breeding season in November (Figure 2.11). Female excursions were least common in the summer months when fawns were young, but were a regular occurrence the rest of the year.

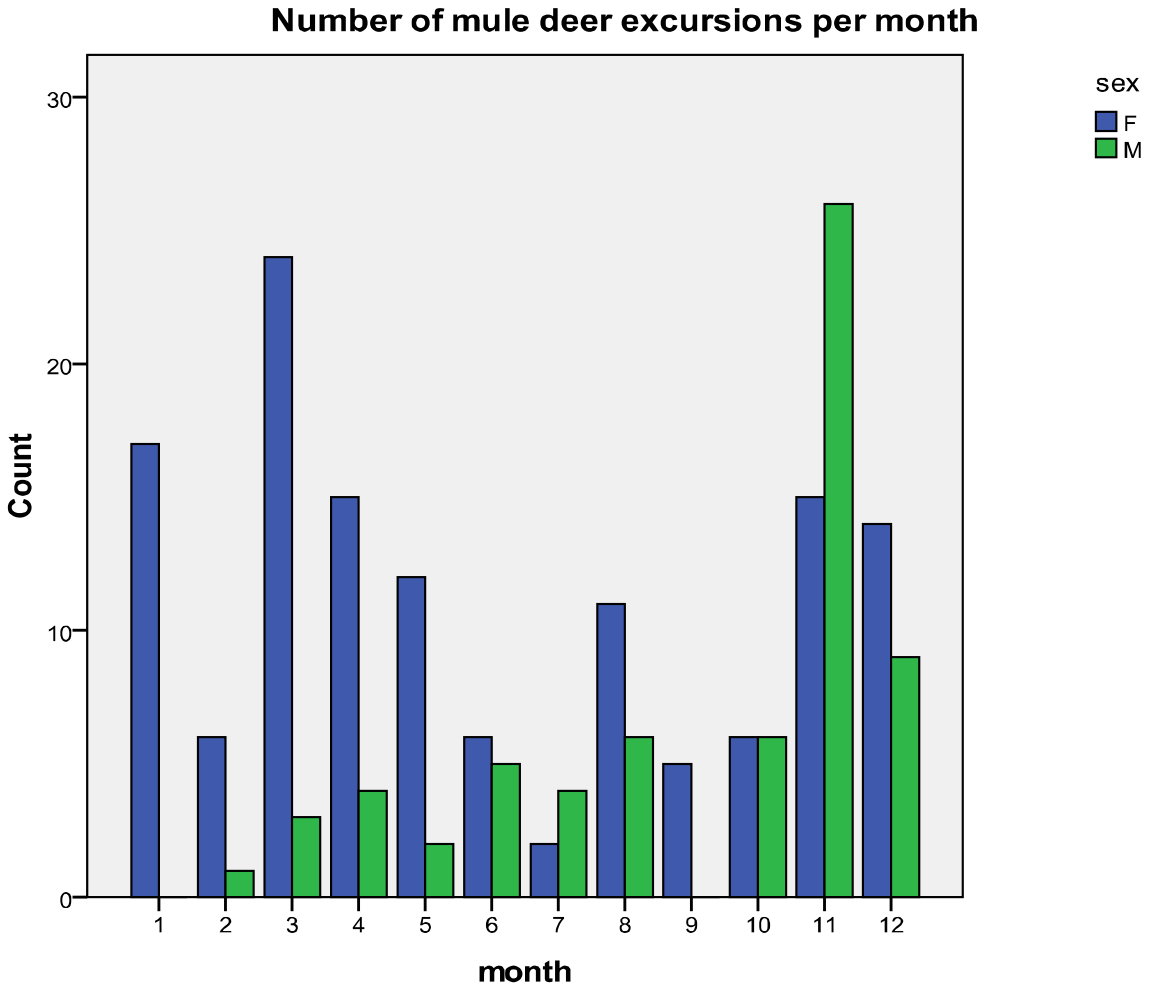

Figure 2.11: Count of excursions made by mule deer for each month. All years of data were pooled.

Most excursions were of short duration (Table 2.7). Female movements outside the range were most often less than a day and male were 1 day (Figure 2.12). Duration was significantly different between sexes ($Z_1 = -4.368$, $P \leq 0.001$).

Table 2.7: Period (days) of excursion by sex.

sex	Mean	*n*	Median	SE	Range
F	2.62	133	.00	.569	31
M	4.41	64	1.00	.983	27
Total	3.20	197	.00	.502	31

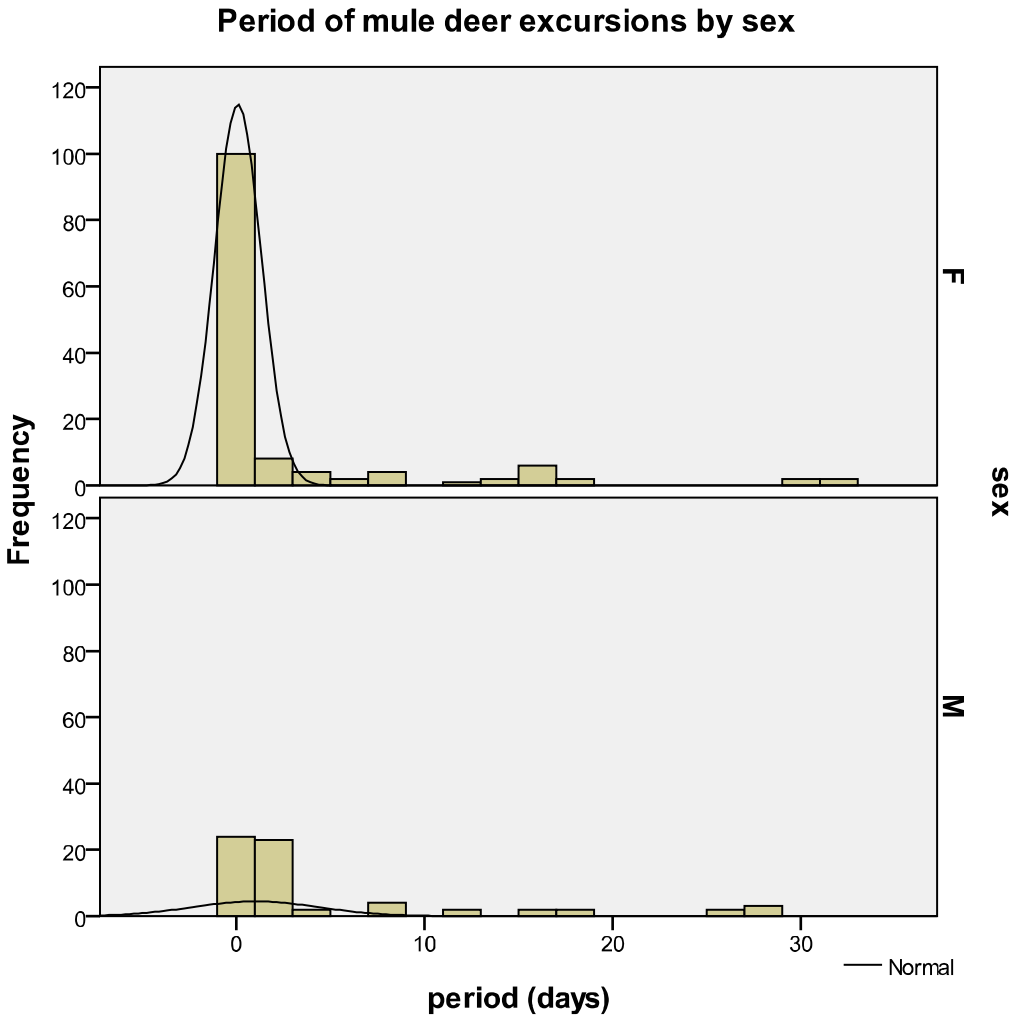

Figure 2.12: Period (days) of mule deer excursions by sex, showing non-normal distribution.

The South Saskatchewan River appeared to be somewhat of a barrier to dispersal and migration movements, but not to all deer. Six individuals crossed the S.S. River one time, an additional 4 crossed twice, and one individual crossed 4 times. Five were from ANT, 4 from SWI, and 1 each from MAT and DOU. River crossings occurred at various times of year. Within the study site, the S.S. River is approximately 1 km wide.

2.4.2 Attributes of Long Distance Movements

2.4.2.1 Travel speed

The average travel speed of dispersal was calculated from 5 GPS-collared dispersing juvenile deer at 769 m/hr (SD= 506; range: 1–2819 m/hr). Three of these juveniles dispersed over a short period (3–48 hours) and 2 juveniles dispersed over a longer period (9–15 days) that involved some days of rest (Table 2.8).

Table 2.8: Travel speed and duration of dispersal for GPS-collared mule deer.

deer_ID	Average m/hr	Max m/hr	Min m/hr	Elapsed hr	Fix interval (hr)	Days
O010	1420	1697	1250	3	1	0.1
O016	187	1238	1	356	4	14.8
O053	775	1595	151	48	6	2
O057	373	2819	24	224	6	9.3
Y024	1092	2706	77	28	1	1.2
overall	769	2011	301	132	4	5.5
SE	226	317	239	68	1	2.8
SD	506	708	534	153	3	6

The average travel speed of migrating mule deer calculated from 28 GPS-collared adults was 1039 m/hr (SD=366; range 5–4162 m/hr). Most migrations took place in less than a day (Table 2.9).

Table 2.9: Travel speed and duration of migration for GPS-collared mule deer.

deer_ID	Average m/hr	Max m/hr	Min m/hr	Elapsed hr	Fix interval (hr)	Days
B022	807	1539	76	4	4	0.2
B029	710	2101	77	52	4	2.2
B049	727	1492	63	20	4	0.8
B050	1260	1993	527	8	4	0.3
B064	623	1267	285	28	4	1.2
G030	1052	1238	865	8	4	0.3
G032	721	1230	178	12	4	0.5
G034	779	2004	142	104	4	4.3
O003	366	436	291	12	4	0.5
O045	1490	3505	130	30	1	1.3
O055	637	932	342	16	6	0.7
P042	1170	1789	300	5	1	0.2
P045	1506	1992	1137	4	1	0.2
P051	1258	1666	851	2	1	0.1
Y022	1088	1921	609	12	4	0.5
Y026	1436	2391	480	8	4	0.3
Y057	1118	1254	983	8	4	0.3
Y060	1299	2786	433	12	4	0.5
Y063	1200	3117	233	16	4	0.7
Y064	734	2371	71	52	4	2.2
Y066	598	1718	15	56	4	2.3
Y067	760	3226	26	52	4	2.2
Y076	1081	2148	15	4	4	0.2
Y078	809	1881	5	40	4	1.7
Y058	1434	2417	133	8	1	0.3
P012	1932	4162	137	108	1	4.5
P041	991	2528	24	81	1	3.4
P052	1517	2674	791	7	1	0.3
overall	1039	2064	329	27	3	1.1
SE	69	154	62	6	0	0.2
SD	366	817	330	30	1	1

2.4.2.2 Travel orientation

Mean dispersal direction was 49° (SD= 79°, median = 60°, 95% CI: 351°–108°). Rayleigh's uniformity test was not significant ($Z = 2.138$, $P = 0.117$, $n = 14$) but Rao's test results indicated spacing was not uniform ($U = 219.14$, $P < 0.01$, $n = 14$). Figure 2.13 shows directional tendencies around the compass. The southwest quadrant appears to have been avoided. From DOU or MAT, southwest travel would require deer to cross the S.S. River; from ANT, BEE, or SWI, southwest travel would lead into land dominated by agricultural activity with little suitable habitat.

Mean vector of migrations was 41° (SD = 92°; median = 47°, 95% CI: 2°–79°). Migration direction distribution was not uniform (Rayleigh's $Z = 4.137$, $P = 0.016$, $n = 55$), nor was spacing uniform (Rao's $U = 177.7$, $P < 0.001$, $n = 55$). Study site migration bearings were not significantly directional except for BEEMAT (Rayleigh's $Z = 6.9$; $P < 0.001$; Rao's $U = 194.6$, $P < 0.01$; $n = 33$). Mean migration vector at this site was 35° (SD = 72°; median = 27°; 95% CI: 6°–63°) (Table 2.10). Sample sizes for the other sites were low, meaning these directionality tests have limited use, and the overall mean direction was strongly influenced by migratory deer in BEEMAT. Direction of travel was randomly and evenly distributed for excursions (Rayleigh's Z = 0.26, $P > 0.7$; Rao's $U = 132.87$, $0.50 > P > 0.10$; $n = 56$).

Table 2.10: Mean migration vector by study site. Only BEEMAT had significant directionality.

site	DOU	BEEMAT	ANT	SWI
n	6	33	6	10
Mean Vector (μ)	231°	35°	103°	235°
Median	180°	27°	86°	291°
SD of Mean	128°	72°	86°	148°
95% CI (-/+) for μ	*****	6°		*****
	*****	63°		*****

***** indicates that a result could not be calculated.

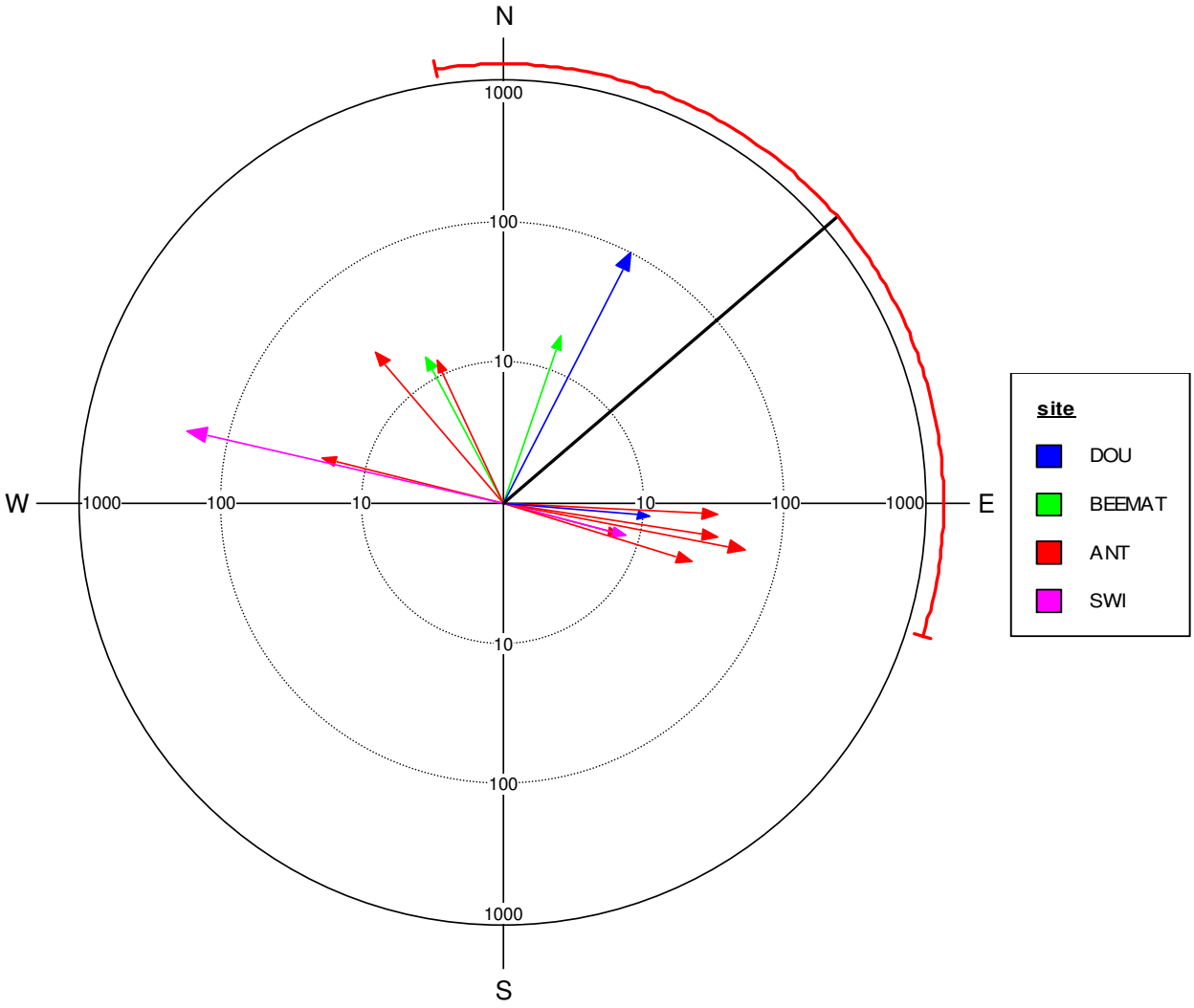

Figure 2.13: Distance and direction (km) of dispersal events. Distance scale is logarithmic. The black line on the compass represents overall mean direction (49°) with 95% confidence interval shown in red. Directionality was not significant but directions were significantly clustered about the compass.

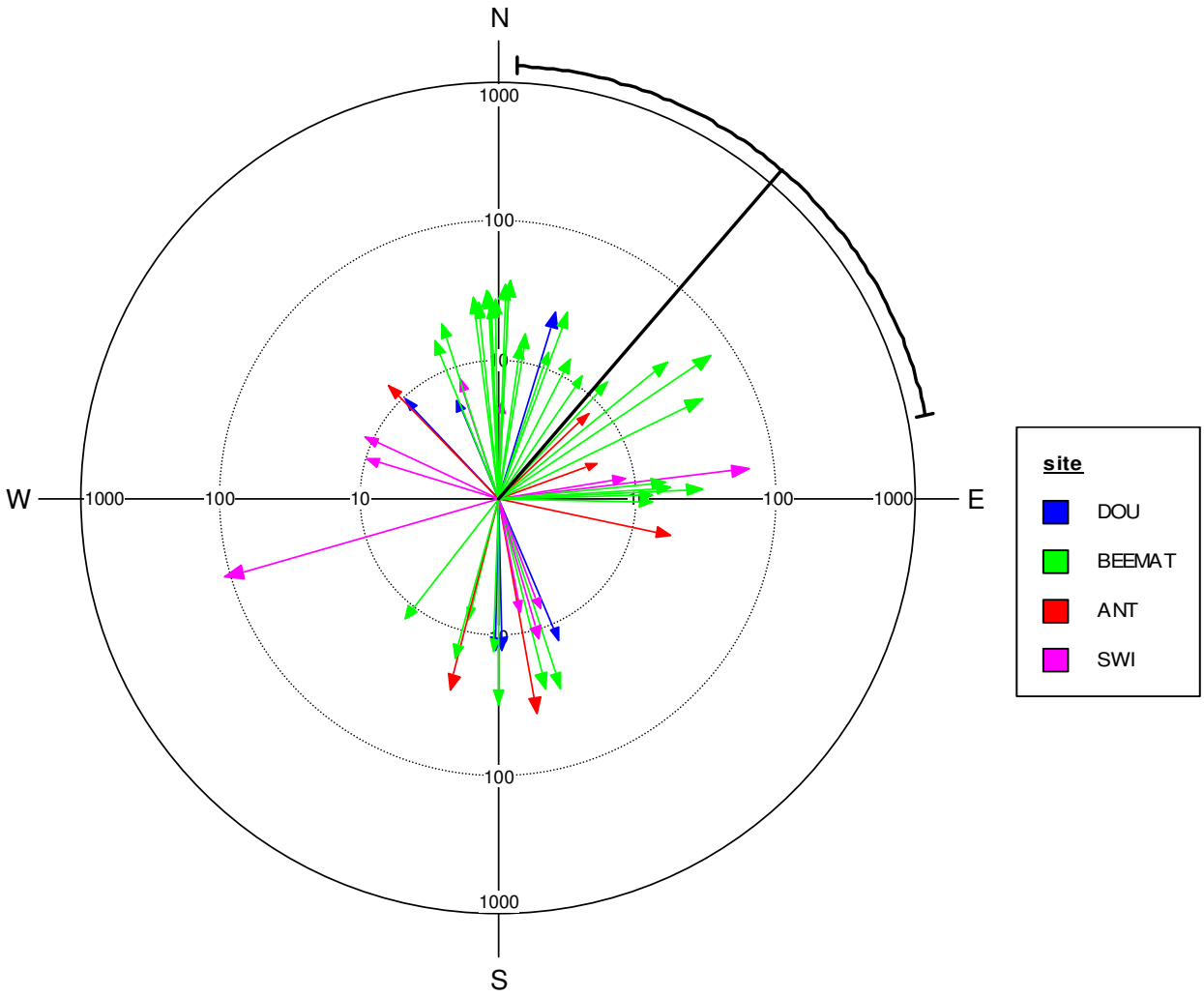

Figure 2.14: Distance and direction (km) of migration events (1 per deer). Distance scale is logarithmic. The black line on the compass represents overall mean direction (41°) with 95% confidence interval.

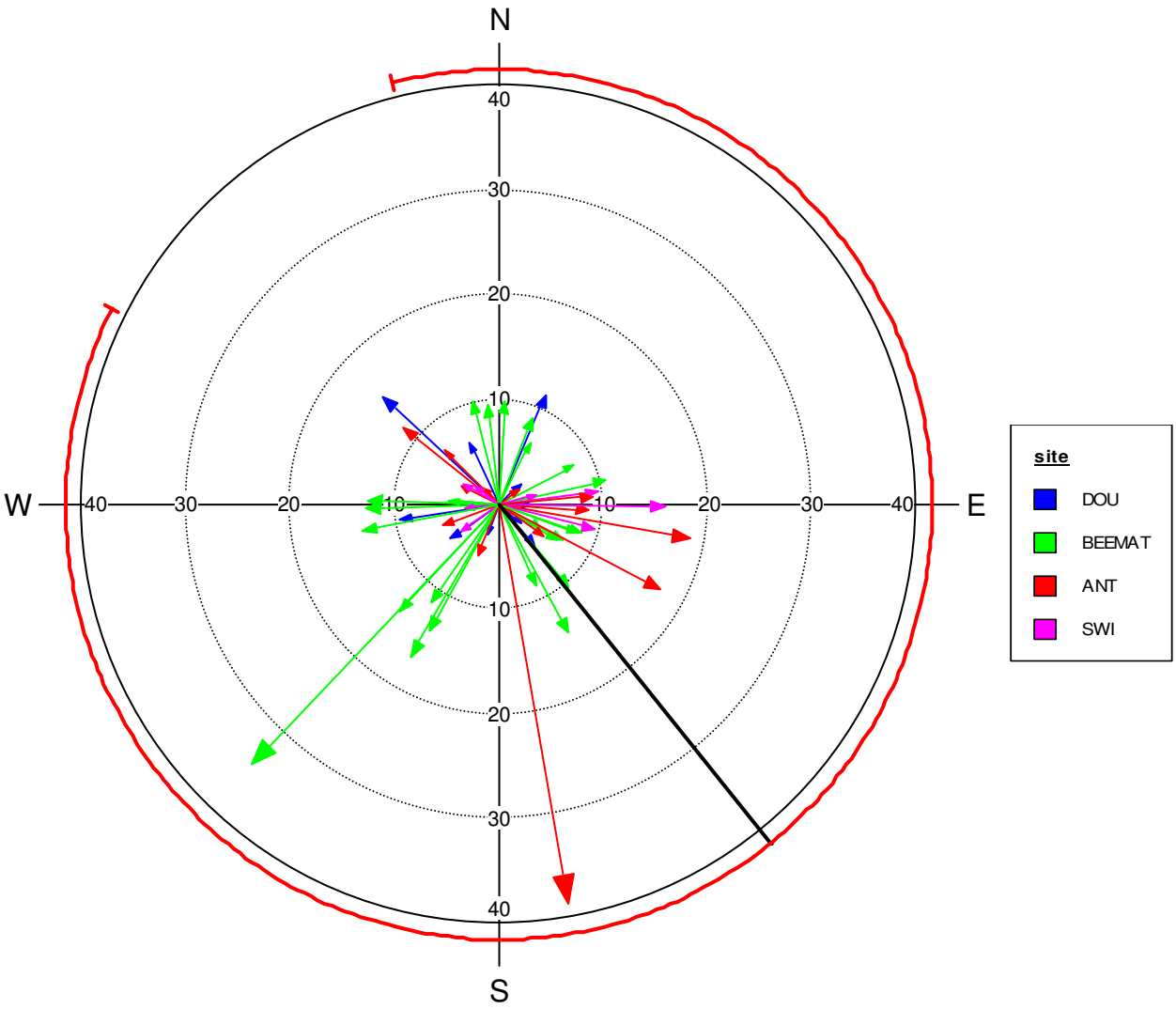

Figure 2.15: Distance and direction (km) of excursion events (1 randomly selected per deer). The black line on the compass represents overall mean direction with 95% confidence interval shown in red. Direction of movement was not significant for excursions.

2.4.2.3 Habitat selection

The most parsimonious model for chosen travel path on long distance movements included selection of habitats with rugged terrain and in close proximity to grassland. Terrain ruggedness held the strongest influence. We expected an autoregressive structure would best fit the data, but QIC values indicated an exchangeable structure was most appropriate. Competing models included proximity to water and grid road, but their regression coefficients approximated zero and QICC values on these models suggest the main model is the only appropriate fit to the data (Table 2.11).

Table 2.11: GEE model results

	Model							
	1				2			
			Interval				Interval	
Parameter	*P*	β	lower	upper	*P*	β	lower	upper
TRI_1	0.001	0.190	0.077	0.302	0.000	0.229	0.110	0.347
Grass $dist_2$	0.000	-0.002	-0.003	-0.001	-	-	-	-
correlation structure	EXCH				EXCH			
QIC	2558.42				2634.55			
QICC	2509.20				2590.30			
ΔQICC	0.00				81.11			

Note: parameter meanings: 1. TRI = Terrain ruggedness index, 2. Grass dist = distance to nearest grassland

2.5 Discussion

2.5.1 Long Distance Movement Demographics

Dispersal and migration occurred frequently in our study population, and there was no significant difference in mean distance moved for the two movement types. The longest dispersal distance was 195 km by a juvenile male and the longest migration distance was 113 km by an adult female. For comparison, the longest mule deer dispersal reported in south-central

Washington was 113 km (Hedlund 1975) and longest mule deer migration in a mountainous region of western Wyoming was 158 km (Sawyer et al. 2005). A number of adult deer made unidirectional long-distance movements, suggesting adult dispersal may be more common than previously thought. Most migratory deer were from the BEEMAT site where there were large uninterrupted areas of native grassland.

Due to concerns that herd reduction programs were resulting in a shift in population structure toward yearling males and a subsequent increase in dispersal rates, we originally intended to contrast dispersal distances and rates within and outside CWD management areas. Initially the study design included 2 study sites in wildlife management zones (WMZ) outside of CWD herd-reduction zones (BEE and DOU) and 2 sites within (MAT and SWI). In the study's pilot year, we determined mule deer commonly migrated between BEE and MAT and the BEE area was subsequently included in the herd reduction zone. ANT was added as a study site in 2007; it too was within the herd reduction zone. Due to changing boundaries of herd reduction zones and low sample sizes of juvenile deer the goal of contrasting dispersal rates between herd reduction zones and non-herd reduction zones was not met.

Long distance movements were made by adults, as well as juveniles, and there was no difference between migration and dispersal rates or distances. Consequently dispersal and migration movements by mule deer have similar potential for spreading disease across landscapes. However, since adult male mule deer have higher CWD prevalence (Grear et al. 2006), their movement patterns may pose a greater risk for CWD spread.

2.5.2 Habitat and Long Distance Movements

Habitat composition on the landscape seemed to predict movement frequency and direction. Migrations occurred less frequently and were of shorter distances in fragmented, agricultural landscapes. Orientation of migration was predictable in BEEMAT only; otherwise,

deer tended to follow the orientation of the S.S. River. Migration strategies vary among mule deer within their range in North America; in mountainous areas most are migratory, in the prairies, some are migratory. Although theories on migration strategies differ, Mackie et al. (2003) succinctly stated "movement patterns employed by individual deer depended on the spatial arrangement of habitat components they attempted to exploit."

Juvenile dispersals were frequent on the south side of the S.S. River but the low sample size of juveniles from BEEMAT limited the confidence in prediction of dispersal rates from a less fragmented grassland habitat. A study of white-tailed deer found that dispersal distance increased in habitats with less forest cover, but that dispersal rates were independent of forest cover and population density (Long et al. 2005). Source-sink models and island biogeography theory predict that patches of ideal habitat separated by large distances are less likely to be colonized (Noss and Csuti 1997). Landscape characteristics between fragments of suitable habitat are important in the dispersal process; however, their effects are poorly understood and are likely species-specific (Wiens 2001). The amount and arrangement of ideal rugged grassland habitat within a landscape may predict mule deer dispersal distance, but a larger sample size is required in order to make this conclusion. Habitat preference and habitat availability in a landscape can easily be measured and there is increasing evidence landscape can be used to predict dispersal orientation.

In this study, like many others, observations on dispersal consisted of only x, y locations and lacked measurement of behavioral cues or other factors that may contribute to a dispersal event. Research on factors influencing dispersal rate is a formidable task given the cost of acquiring an appropriate sample size and measuring multiple demographic, landscape, and social

parameters. In this study, similar to others, males were more likely to disperse, and approximately half the surviving juveniles dispersed.

2.6 Management Implications: CWD and Long Distance Movements

2.6.1 Mule Deer

Surveillance data show that CWD positive mule deer are most often in wildlife management zones adjacent to the S.S. River (CCWHC, unpublished data). Preliminary analyses suggest the probability of harvesting a CWD-positive deer in Saskatchewan increases with terrain ruggedness, proximity to major rivers and distance to roads (Rees et al. 2009). It is generally suspected that the S. S. River basin plays a role in spread of disease westward through Saskatchewan and into the neighboring province of Alberta. Although proximity to water was not a significant factor in long distance movement paths when tested in the GEE, terrain ruggedness and grassland proximity were significant and both are attributes associated with the S. S. River. Coulees with dramatic inclines and grassland unaltered by agricultural practices exist along the River basin and provide the rugged terrain that is a key mule deer habitat requirement (Wood et al. 1989, Dusek 1975). Pearson's correlation scores for terrain ruggedness with distance to grassland and distance to water were -0.244 and -0.181 respectively, suggesting that rugged terrain and wetlands were found not only along the river but also interspersed throughout the landscape.

Miller et al. (2000) speculated that the CWD epidemic in Colorado and Wyoming corresponded to patterns of mule deer migration along the North and South Platte Rivers. Long distance movements by white-tailed deer were found to be directional according to the orientation of a major river in Montana (Dusek et al. 1989) and South Dakota (Kernohan et al. 1994), and aligned with ridged topography (but not rivers) in Pennsylvania (Long 2006).

Jacques et al. (2003) suggested that CWD spread in South Dakota would be hastened by white-tailed deer movements along river-bottom habitats.

In this study, mean migration orientation was 41°, roughly perpendicular to the orientation of the S.S. River at the BEEMAT site. Disease spread in a northeastern direction from CWD-positive foci alongside the River has not been systematically evaluated using surveillance data but new cases have been found further north from the River in recent years. This suggests migrating deer may play a role in disease spread in a northeastern direction, but disease transmission is more efficient in mule deer habitat along the River basin itself, perhaps due to seasonal differences in mule deer grouping behavior.

Mule deer congregate in larger groups and smaller areas during winter months (Wood et al. 1989, Lingle 2003, Conner and Miller 2004). In the BEEMAT study area, deer moved to the coulee habitat along the river in cold winter months and were more spatially separated in spring and summer (Silbernagel, 2010). A few adult males were an exception—they summered along the river, migrated north in autumn and stayed there until spring. Silbernagel (2010) also analyzed GPS data of mule deer in this study and found that proximity between collared deer was highest during winter months. CWD transmission risk is likely higher along the River during winter months because deer are in higher density, and share a limited number of forage locations. Deer that migrate from densely-populated wintering areas may carry disease to their summering ranges.

Recent studies have shown that contact with prion-contaminated environments is an effective mode of CWD infection (Miller et al. 2004, Johnson et al. 2006, Mathiason et al. 2009, Wiggins 2009). Further investigation into the role of prion-contaminated soil in CWD-endemic areas like the S. S. River basin would greatly enhance our understanding of CWD transmission.

2.6.2 White-tailed Deer and CWD in Saskatchewan

Although our observations of white-tailed deer movements were limited, we speculate the risk of geographic spread of CWD is substantial for this species, and less predictable than for mule deer in the Mixed Grassland. In 1972–74, a mark-recovery study (Stewart and Runge 1985) of white-tails in the Crystal Beach Game Preserve (CBGP) of central Saskatchewan showed high emigration of juveniles (fawns or yearlings) and long travel distances ($\bar{x} = 215$ km). The farthest recovery was a yearling doe found in southwest Manitoba, 673 km southeast of its natal site. Over 30% of recovered deer trapped as juveniles were located >50 km from the study area, whereas only 1 of 19 adult-tagged deer was recovered >5 km from the study area. No significant directionality of movement was noted. There may have been avoidance of travel along the major highway in the area, but it was not a barrier to movement. Seven deer were located across the South Saskatchewan River to the east and south of the study area. The results of this study showed no barriers to white-tailed deer movement and presumable ease of disease transmission throughout the species' range of Saskatchewan, and beyond into neighboring provinces and states.

Our model results suggested that mule deer movement can be predicted by variables such as rugged terrain and grassland and it follows that habitat preferences could be similarly used to predict white-tailed deer movement. Since white-tailed deer are better adapted to agricultural land than are mule deer, their movement may be less limited in Saskatchewan. Chronic wasting disease prevalence in Wisconsin white-tailed deer is related to abundance of deer habitat (Joly et al. 2006). Wood, Mackie, and Hamlin (1989) studied sympatric mule and white-tailed populations in Montana prairies and found compared to mule deer, white-tailed deer used grain fields more frequently, were generally more mobile, had larger home ranges, and had less fidelity to traditional home ranges. Our observations of white-tailed movement patterns were

similar. In recent years a focus of CWD has developed in white-tailed deer in north-central Saskatchewan near Nipawin (53.37°N, -104.01°W), in the Boreal Transition ecoregion and in proximity to the Saskatchewan River. While our study results cannot be applied to this area, there are recent examples in the literature of white-tailed movement patterns and habitat preferences being used to predict long-distance movements (Felix et al. 2007, Diefenbach et al. 2008, Frost et al. 2009).

CHAPTER 3
MULE DEER (*ODOCOILEUS HEMIONUS*) SURVIVAL RATES IN A CWD-ENDEMIC AREA OF SOUTHERN SASKATCHEWAN

3.1 Abstract

Chronic wasting disease (CWD) has been detected in wild mule deer (*Odocoileus hemionus*) of southern Saskatchewan since 2000 and continues to increase in geographic range and prevalence. Management programs for the disease continue to evolve but have focused primarily on herd reduction in known CWD areas. Deer survival rates have not been measured in these areas and have been impacted by management decisions in recent years. Chronic wasting disease will likely affect survival rates in the long term. Survival analyses were completed in concurrence with a radio telemetry mule deer movement study from 2006–2009. Adult deer mortality occurred primarily during hunting season but at differing rates between sexes depending on the year and management program. Juveniles (up to 2 years old) had lower survival rates than adults and they experienced higher mortality during the summer period following capture. Radio collar mass contributed to their poor survival and in the future researchers should use a collar that is a maximum of 2% of body mass. Deer in good body condition were half as likely to die and deer in very poor body condition were twice as likely to die. Home range habitat content did not appear to affect survival. Mule deer survival in Saskatchewan was influenced primarily by harvest regulations. In the future, as CWD prevalence increases, disease impacts on survival rates can be measured and compared to current survival rates.

3.2 Introduction

Chronic wasting disease (CWD) was first detected in a wild mule deer (*Odocoileus hemionus*) in Saskatchewan, Canada in 2000. The disease is contagious, fatal, difficult to manage, and it continues to threaten wild cervids over an ever-expanding range within North America. Long-term impacts of CWD on host populations are unclear but will depend on other factors such as recruitment and other sources of mortality. Age and cause-specific mortality rates of deer are required in order to predict the effect of CWD on deer populations.

Only a few recent studies have estimated the effect of CWD on deer populations. In Colorado, where localized CWD prevalence in mule deer was 41% in adult males and 20% in adult females, Miller et al. (2008) found that CWD-infected individuals had poorer survival than their uninfected counterparts, and that mountain lions (*Puma concolor*) selectively preferred CWD-infected mule deer prey. Prior to that publication, studies evaluating impacts of CWD on deer populations were based on theoretic models which predicted population declines and possible host extinction (Miller et al. 2000, Gross and Miller 2001). Models are helpful when decisions must be made with best available knowledge, but assumptions should be rigorously evaluated and models revised and adapted as new knowledge becomes available (Schauber and Woolf 2003).

In North America, deer survival is affected by hunting, winter severity, disease, predation, vehicle collisions, interspecific competition, habitat changes, population density, and natural causes (White et al. 1987, Wood et al. 1989, Unsworth et al. 1999, DelGiudice et al. 2002). Deer experience seasonal gains and losses in body mass, depending on metabolic needs and range conditions, and their body condition can affect their survival during strenuous winter months (Mackie et al. 2003, Klaver et al. 2008). Our objective was to estimate mule deer survival patterns and rates in southern Saskatchewan and to estimate the role of potential factors

on survival. Factors were classified as intrinsic, consisting of measures of body size and condition, and extrinsic, consisting of characteristics of the home range which may affect survival. The impact of radio collars on survival was also addressed. This study contributes to our understanding of the impact of CWD on local deer population demographics, and the effects of radio marking on deer survival.

3.3 Methods

3.3.1 Study Area

Refer to section 2.3.1 for study area description.

3.3.2 Capture

Refer to section 2.3.2 for capture methods.

3.3.3 Radio Collars

Throughout the course of the research project, we used 4 different types of radio collars. We began with one type of VHF and one type of GPS, weighing 425 g and 900 g respectively. After the first year we decided to compromise on battery life in order to use lighter weight collars on juvenile deer (a different type of VHF and GPS, weighing 200 g and 300 g respectively). Mortality seemed disproportionately high for juveniles with GPS collars in the first year they were captured (2007). The cause was unclear but it could have been an effect of increased predation, or added stress at a crucial time of year. We followed animal care protocol guidelines by using collars weighing less than 5% of the deer's body mass (Canadian Council on Animal Care 2003), but felt that the radio collars were having a notable adverse effect on survival in smaller-bodied deer and warranted investigation.

3.3.4 Body Condition Index (BCI)

Body condition refers to an animal's energetic reserves in fat and muscular tissue, and is measured by its mass relative to its structural size (Cattet 2000, Schulte-Hostedde et al. 2005).

Beginning in 2007, each deer's mass was measured to the nearest kg using a cot hung from a scale on a tripod. Body size was measured to the nearest cm for chest girth, hindfoot length (Parker 1987), neck circumference, and total body length (Bois et al. 1997, in Lesage et al. 2001). Deer were laterally recumbent for all measures. We derived the 4 log-transformed measures into a single body size value (PC1) using principle components analysis in SPSS (version 17.0; SPSS Inc., Chicago, Ill.) (Schulte-Hostedde et al. 2005). Prior to calculating the PC1 or BCI, we assessed the dataset for outliers in measurements, and removed one deer with an obvious erroneous hindfoot length measurement and also removed 18 deer (captured in 2008) with questionable mass measures because it was noted the scale had not been properly zeroed.

We assessed correlation of body mass and body size for linearity. If PC1 was positively related to all body size measures, it was a good indicator of size (Dobson 1992, Schulte-Hostedde et al. 2001, 2005). Body condition scores were the standardized residuals of the regression of body size and body mass (Cattet et al. 2002, Schulte-Hostedde et al. 2005).

Each deer's BCI score was used as a covariate in Cox regression. We also tested for thresholds in body condition by assigning BCI scores to poor (25^{th} percentile), mid, and good (75^{th} percentile) categories. If these thresholds were non-significant, we tested a more extreme threshold: very poor (10^{th} percentile) or very good (90^{th} percentile).

A *t*-test modified for unequal variances was used to detect difference between 2007 and 2008 BCI.

3.3.5 Home Range Attributes

3.3.5.1 Land cover classification map

With assistance of remote sensing specialists, we developed a land cover map of the study area using 20 m multispectral SPOT (Satellite Pour l'Observation de la Terre) imagery (Alberta Terrestrial Imaging Centre, Lethbridge, AB, T1J 0P3). Three images taken in July 2007

encompassed the ANT, BEEMAT, and SWI sites, and an image taken September 2007 included the DOU site. The latter image was classified separately because of spectral differences due to vegetative phenology. PCI Geomatica software (PCI Geomatics, Richmond Hill, ON, L4B 1M5) was used to orthocorrect raw imagery.

Training data were collected throughout June, July, and August 2007 on transects walked during deer surveys. At regular intervals, observers recorded GPS locations and dominant vegetation types within 20 m. Additional training data were acquired through visual interpretation of the satellite imagery, aided by our knowledge of the area and confirmed with high resolution (2.5 m) panchromatic SPOT imagery (Telus 2006). We retained 30 percent of the training data for accuracy assessment. Overall accuracy was 90% for the DOU site and 91% for the other sites (see appendix A).

Topographic data were stacked with the imagery to assist in classification: a 25 m digital elevation model (Government of Canada, Centre for Topographic Information) and terrain ruggedness raster (TRI) (Evans 2004). A homogeneity filter was applied to the near-infrared band of the SPOT imagery to better delineate vegetative areas. Supervised classification was performed in ENVI 4.5 software (ITT Visual Information Solutions, Boulder, CO 80301) using a maximum likelihood classifier. Pixel values overlapped for some classes identified in the training data and were not discernible by the software (e.g., forage crops were similar to annual crops). These were lumped into simpler classes, resulting in a final classification scheme of 4 classes: crop, grassland, wetland (including open water) and shrub or woodland. The crop class included fallow unvegetated fields.

3.3.5.2 Home range calculation

Home range polygons were calculated as 95% kernel density estimates (KDE) (Rodgers et al. 2007) in ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, Calif.). Least

squares cross validation (LSCV) was used as a smoothing factor for VHF-collared deer with suitable sample sizes (> 10 or < 100) (Hemson et al. 2005). GPS-collared individuals had sample sizes > 100 and for these 275 m was selected as a smoothing factor because h*ref* (software-generated reference bandwidth) tends to over-smooth and inflate home range size (Seaman et al. 1999).

Home ranges were intersected with the land cover, digital elevation, and TRI data to estimate habitat covariates for each deer. Mean elevation, mean terrain ruggedness, and proportion of grass, shrub, wetland, and crop within home range were calculated.

3.3.6 Statistical Analyses

3.3.6.1 Dataset

Deer that were lost to follow-up because of collar loss, collar failure, failure to locate, or those still collared at the end of the study period were right-censored, and those that died within 21 days of capture were excluded from analysis. Studies often exclude deaths within a short period of capture, often 14 days but ranging from 7 to 26 (Lawrence et al. 2004, Farmer et al. 2006, Grovenburg 2007). We selected 21 based on the frequency of telemetry signal checks post-capture. Mortality signals were investigated as soon as possible; however, cause of death was often unknown due to scavenging. Death was confirmed by finding carcass remnants at the collar site, including scavenged carcass, hair, bones, or blood. Collars found without any remnants were usually fully-expanded VHF collars or were from loosely-collared juveniles and these were considered to be slipped collars and not deaths. For each deer, the time (in months) between capture and last observed live signal was used to calculate the research lifespan.

3.3.6.2 Kaplan-Meier estimates

Annual and seasonal survival rates were calculated following the Kaplan-Meier (K-M) procedure (Kaplan and Meier 1958) modified for staggered entry of animals (Pollock et al.

1989). Survival estimates were calculated for 2006, 2007 and 2008 for adult females and for 2007 and 2008 for adult males. Survival estimates for juveniles were calculated for the first (2007) capture cohort only, as the sample size (n = 11) of the second cohort in 2008 was low. Annual survival was from April to March and seasons were divided into hunt (September to December), winter (January to April) and summer (May to August). We identified a winter period by its latter year (e.g., 2007 for the 2006–2007 winter). Differences in survival functions between groups were tested by log-rank chi-square statistics (Pollock et al. 1989): specifically, we used the generalized Wilcoxon test (an adaptation of the log-rank test that weights by the number of at-risk individuals per interval) (Breslow 1970, Hosmer and Lemeshow 1999). The log-rank test is appropriate when hazards are proportional (i.e., hazard lines do not cross) (Collett 2003). If they are not, a test developed by Breslow (1984) accounts for acceleration and is appropriate. *Z*-tests are used to compare 2 survival curves at a particular time (Pollock et al. 1989). α was set at 0.05. Comparisons between sexes included only adult deer because sexes were pooled for juvenile datasets.

3.3.6.3 Cox regression

Covariate effects on hazard rates were tested using Cox proportional hazards regression model (Cox 1972) in PROC PHREG (version 9.2; SAS Institute, Cary, NC) (Allison 1995). The Cox model is described by the equation:

$$h_i(t) = \lambda_0(t)\exp\{\beta_1 x_{i1} + \ldots + \beta_k x_{ik}\},$$

Meaning the hazard (h) for individual i at time t is the product of:

(1) $\lambda_0(t)$ which is the baseline hazard experienced by all animals, and

(2) the exponentiated linear set of k covariates.

Thus we can derive the expected hazard rate at any time (t) for any individual (i) with knowledge of its covariates.

Survival analyses were completed at 3 levels with different sample sizes depending on the variables tested. We used the full dataset to test significance of basic variables: age (in years, at capture time), age class (juv or ad), capture type (helicopter or trap), collar type (GPS or VHF), and capture year. In addition, we examined 2 subsets of the deer for different risk factors: intrinsic and extrinsic factors.

Intrinsic variables included body condition, body mass, and ratio of radio collar mass to body mass. We categorized body condition into percentile thresholds (Table 3.1). Three broad categories (1^{st}, 2^{nd} + 3^{rd}, and 4^{th} quartiles) were tested first, and if there was no effect at that level then thresholds at the 10^{th} and 90^{th} percentile were tested. We categorized collar-to-body-mass ratio into less than or greater than 2% of body mass. We suspected a higher hazard risk was experienced by small (juv) deer wearing GPS collars, and >2% appeared to fit that subgroup. The intrinsic measures dataset excluded 2006 captures because their body measurements were not recorded and a body condition index could not be calculated.

Table 3.1: BCI categories determined by percentile.

BCI category	Percentile	BCI value
very poor	≤10	≤-1.19
poor	≤25	≤-0.68
mid	26 to 74	-0.68 to 0.61
good	≥75	≥0.61
very good	≥90	≥1.34

Variables in the extrinsic factors dataset included home range parameters: migratory strategy (migratory, resident, or dispersal), average terrain ruggedness (TRI), average elevation, and 4 habitat type proportions: grassland, shrub, crop, and wetland. Deer with fewer than 20 locations were excluded because their home range estimates were not accurate enough and might

bias results.

The Cox model assumes individuals experience proportional hazards through time. Hazard lines that cross for different strata or groups violate this assumption (Hosmer and Lemeshow 1999, Cox 1972). Prior to regression analysis, we used PROC LIFETEST in SAS to visually assess proportionality of survival and hazard lines and then stratified accordingly. Cox regression analyses were performed in SAS. We tested time-dependence of significant variables by including a term representing an interaction between a suspected covariate and time (Allison 1995). The "exact" method was used to handle ties in the dataset.

If none of the covariates explained survival better than the null model (i.e., if $P > 0.1$), then the null model was accepted as the final model. We used forward stepwise regression for inclusion of variables, and AIC values for comparison of models where $\Delta AIC \leq 4.0$ (Burnham and Anderson 2002). Individually-tested variables with P values < 0.2 for their coefficients (β) were included in multivariable analyses, and retained in final models if $P < 0.10$. We chose $\alpha = 0.1$, as is sometimes done in regression analyses when the parameter coefficient (or hazard ratio) is strong but not significant at the 95% confidence level (Johnson 1999, Farmer et al. 2006). If variables were collinear, we selected one based on biological importance. We tested suspected covariates for interactions, including body condition and collar mass. Radio collars may have been an additional stressor for deer in poor body condition and may have exacerbated their mortality rates. Hazard ratios (also known as risk ratios) were estimated for significant variables. Hazard ratios indicate the hazard change per one unit change in the variable (Riggs and Pollock 1992). Most variables were dichotomous so the hazard ratio reflected risk for members vs. non-members of a group. Model P values reported are Wald Chi-square statistics.

Differences in body condition between groups (e.g., sexes, capture years) were detected by *t*-tests. Wellsch's *t*-test was used if Levene's test showed unequal variances. We used chi-square to detect difference in proportions of groups assigned to BCI categories. Significance was set at $\alpha = 0.05$ for these analyses and they were performed in SPSS.

3.3.6.4 Post-hoc winter severity analysis

Winter severity was assessed *post-hoc* to address between-year difference in body condition scores. Body condition was calculated based on measurements at the end of winter, so the data from the months just prior to capture were used to describe winter severity affecting condition at capture time. We obtained Environment Canada data from 3 weather stations located in or near our study sites at Swift Current, Elbow, and Lucky Lake Saskatchewan (Government of Canada 2008). We averaged their daily minimum, maximum, and mean temperatures to represent study area weather. Snow depth data were consistently available for only the Elbow weather station. Winter was described by data from November 1 to March 31. For each day the minimum temperature fell below -20°C, 1 point was accumulated, and for each day snow depth exceeded 10 cm, 1 point was accumulated (DelGiudice et al. 2002, Pitt et al. 2008). Summer precipitation values (from May 1 to October 31) were used to represent forage growth on the winter range (Farnes 1991). For comparison, normal values were estimated using the 30-year average of temperature and precipitation data from 2 of the weather stations. 30-year normal values were not available for the station at Lucky Lake, nor were 30-year snow depth data available for any station.

3.4 Results

3.4.1 Capture

Two hundred and six individuals were included in the survival dataset after removing white-tailed deer, confirmed capture myopathies and those collared <21 days. Of these, 89 deer

died and 117 were censored. Twenty-nine animals died during winter months, 48 during hunting season months, and 11 during summer months. Subsets used for Cox regression had smaller sample sizes: n = 140 for the body condition subset and n = 151 for home range subset.

3.4.2 CWD Results

Six individuals tested CWD-positive at time of capture. All were captured in 2007: 5 were from ANT (4 AD M, 1 AD F) and 1 was from SWI (AD M). One male died within a month of capture and his death may have been capture-related but the carcass was too scavenged for necropsy. The others died within 22 months of capture (range 9 to 22 months) and only one was observed with clinical disease near its death, the others died of unknown cause. Further analysis of the effect of CWD on survival was precluded by the low sample size.

3.4.3 Body Measures

Average body mass of adult females was 61 kg (SD = 9, n = 36); adult males 75 kg (SD = 13, n = 67); juveniles (sexes pooled) 35 kg (SD = 5, n = 80). Further details are found in Table 3.2.

Table 3.2: Body measures of captured mule deer. Juvenile sexes are pooled.

	ADULT MALE		ADULT FEMALE		JUVENILE	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
mass (kg)	75	13	61	9	35	5
chest circumference (cm)	102	6	98	6	79	4
body length (cm)	180	11	169	8	141	8
neck circumference (cm)	46	5	38	3	32	2
hindfoot length (cm)	51	2	48	1	43	2
n	67		36		80	

3.4.4 Body Condition Index

PC1 scores explained 92% of the variance in body size measures. Chest girth was the body measure most strongly correlated with body size (r = 0.97) and all body measurement values contributed to PC1 (Table 3.3). Correlation between body size and mass was high (R^2 = 0.97) (Figure 3.1). The relationship between mass and body size was:

mass (kg) = 19.84 (PC1) + 55.03

Body size and body condition were not related (r = 0.000, P = 0.99, n = 183). Scores below -0.67 were in the poor BCI category (lowest = -2.6), and above 0.61 were in the good BCI category (highest = 3.2) (Figure 3.2). Thresholds for very good and very poor BCI were 1.34 and -1.19, respectively.

Table 3.3: Factor loadings of morphologic measures on PC1 from principle components analysis for mule deer body size

Body Measure	Loading on eigenvector
LN_chest	0.972
LN_neck	0.951
LN_hindfoot	0.956
LN_length	0.961

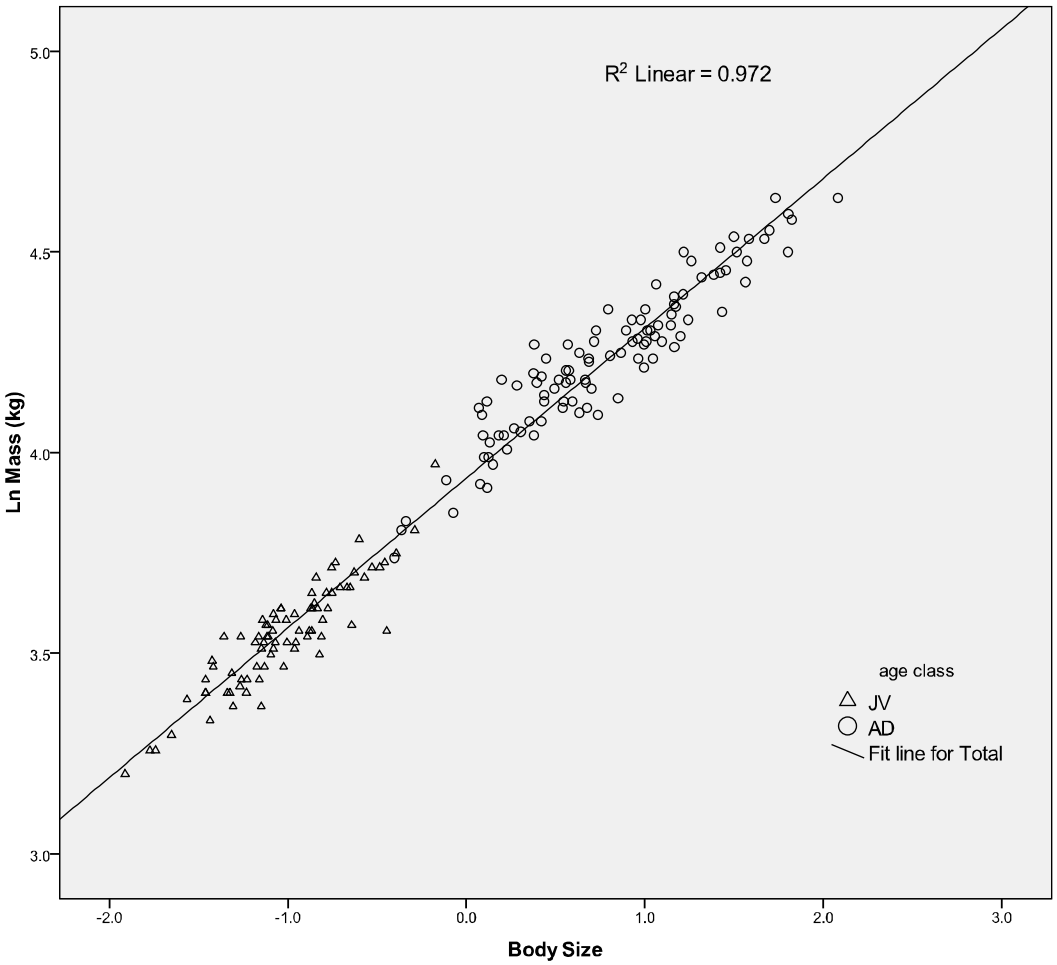

Figure 3.1: Relationship between body size (derived from principle components analysis of 4 body measures) and mass. Juveniles and adults showed similar linearity.

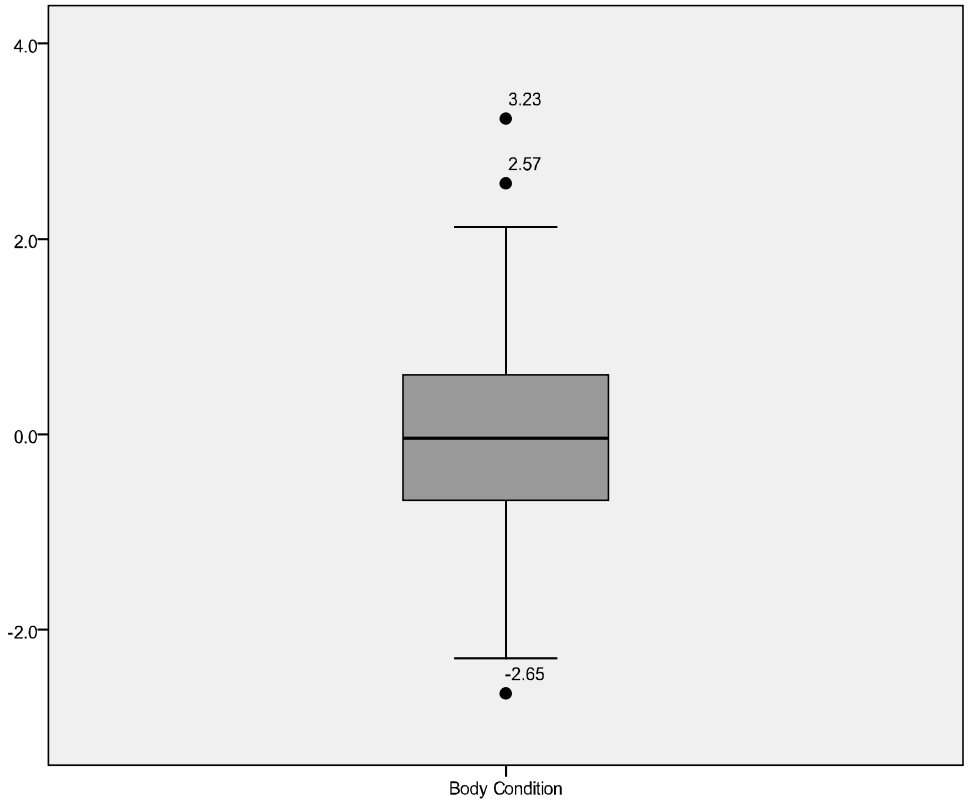

Figure 3.2: Body condition index boxplot. Values below -0.67 and above 0.61 were in the poor and good BCI categories, respectively. Extreme values of 3 deer are also shown.

3.4.5 Radio Collars

The radio collars we used ranged from 0.4% to 3.4% of the deer's body mass at capture time. Most were well within the guidelines: 83% (132 of 159) were under 2% of body mass. Of the 24 deer with a collar >2% of its mass, 14 died and 10 were censored. Eight were in poor body condition, 5 good, and 11 mid. Nineteen were captured by helicopter and 5 by Clover trap. All but one were captured in 2007. Nineteen were juveniles, 4 were yearlings (3 M, 1F), and 1 adult (M). There were 3 from the DOU site (2 ad, 1 juv), and 7 at each of the other sites.

3.4.5 Survival Estimates

3.4.5.1 Kaplan-Meier estimates

3.4.5.1.1 Adults

Annual

Adult female survival was higher in 2008 than in 2007, whereas adult male survival was higher in 2007 than in 2008 (Table 3.4).

Table 3.4: Annual (Apr–Mar) survival rates (SE) of adult male and adult female radio-collared mule deer in southern Saskatchewan, 2006–2008.

Sex	**2006**	**2007**	**2008**
Female	0.76 (0.06)	0.72 (0.05)	0.86 (0.08)
Male	-	0.82 (0.05)	0.62 (0.07)

Seasonal

Adult survival was lowest during the hunting season (Table 3.5), but differences in seasonal survival between years and sexes were observed. In 2006 and 2007, adult does had high survival during the summer, lower in the winter, and lowest in the hunt season. In hunt season 2008, female survival increased to 0.91 (SE = 0.04) and was comparable to survival of previous winters (Figure 3.3). Male survival in 2007 was higher in the hunting season than winter season, but their survival in 2008 was lowest during the hunting season. Male and female survival was not proportional and was similar during summer and winter, so we tested differences between sexes for only hunt seasons 2007 and 2008. In hunt season 2007, female survival was lower than male ($Z_1 = 2.23$, $P < 0.025$) and in 2008, male survival was lower than female ($Z_1 = 2.34$, $P < 0.01$).

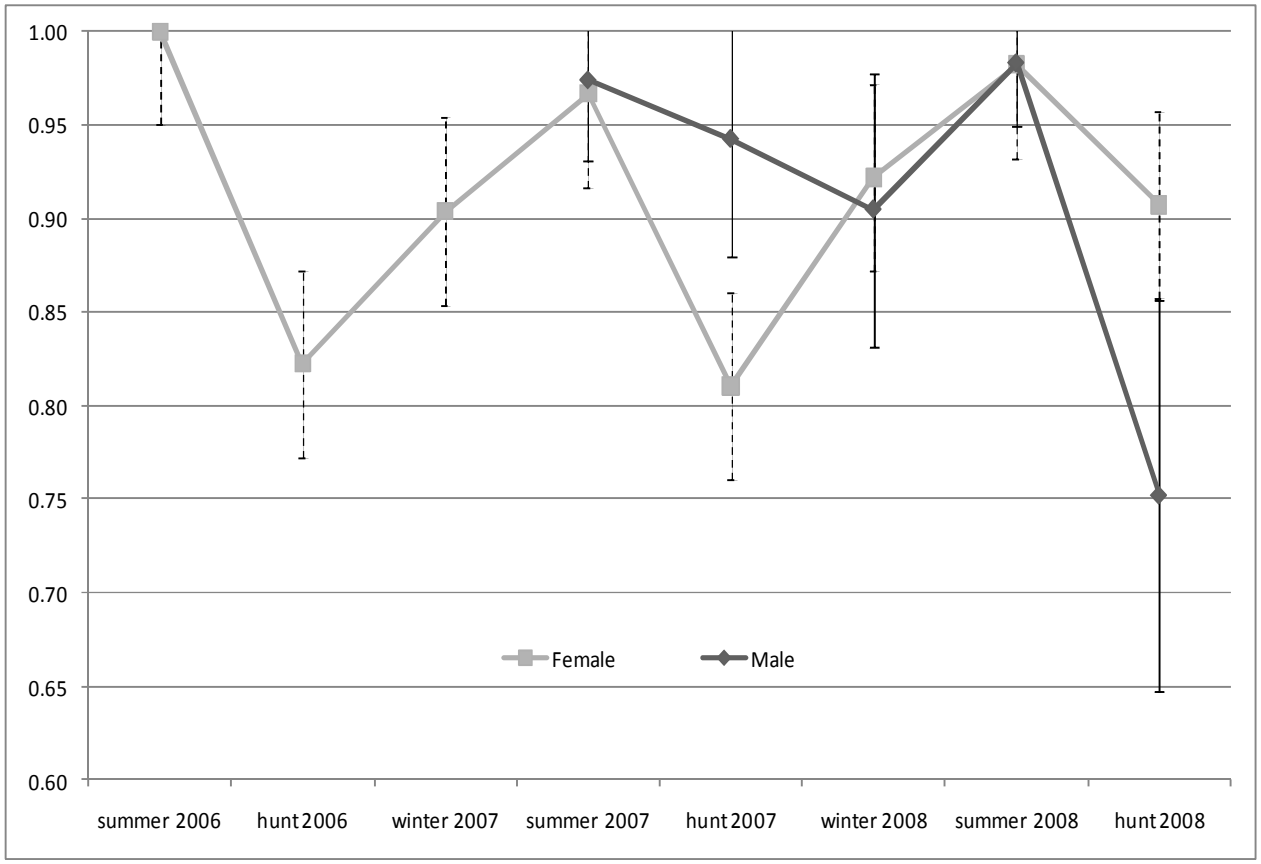

Figure 3.3: Seasonal survival rates of adult female and male mule deer with 95% confidence intervals.

Table 3.5: Adult mule deer seasonal survival 2006–2008. Note the first 3 seasons were female only, otherwise males and females are pooled.

SEASON	SURVIVAL	LOWER 95% CL	UPPER 95% CL
summer 2006	**1.00**	1.00	1.00
hunt 2006	**0.82**	0.71	0.93
winter 2007	**0.90**	0.84	0.96
summer 2007	**0.97**	0.93	1.00
hunt 2007	**0.87**	0.81	0.93
winter 2008	**0.91**	0.86	0.96
summer 2008	**0.98**	0.96	1.00
hunt 2008	**0.83**	0.76	0.90

3.4.5.1.2 Juveniles

Annual

Juvenile annual survival in 2007 was 0.49 (SE = 0.08) and was significantly lower than adult survival in 2007 (0.77, SE = 0.04) ($\chi_1^2 = 13.7$, $P < 0.001$). 2008 juvenile survival rates were poor estimates due to low sample size.

Seasonal

Juvenile survival was lower than adult survival in all 3 seasons, but was only statistically significant in the summer of 2007 ($Z_1 = 2.205$, $P < 0.025$). Survival was 0.81 (SE = 0.07) in the summer following capture (Table 3.6). In contrast, adults experienced very little mortality during summer periods of all 3 years.

Table 3.6: Seasonal survival of juvenile mule deer captured in 2007

SEASON	SURVIVAL	LOWER 95% C.L.	UPPER 95% C.L.
summer 2007	**0.81**	0.67	0.95
hunt 2007	**0.78**	0.62	0.94
winter 2008	**0.86**	0.73	0.99

3.4.6.1 Cox regression

Regression analyses were stratified based on sex and study site because their hazard lines were not parallel. There were no time-dependent interactions of covariates and the variable *Capture Year* was non-significant ($P > 0.6$); therefore, the use of right-censored data was justified despite the staggered entry date of captured individuals.

3.4.6.1.1 Full dataset

Age class was the only variable of significance in the full dataset ($\chi_1^2 = 3.17$, $P = 0.075$). The hazard risk of juveniles was 1.58 times higher than that of adults (95% CI = 0.96–2.60).

This result is comparable to the significant Wilcoxon test of K-M survival curve differences between adults and juveniles.

3.4.6.3.1.2 Body condition subset

Deer in the good BCI (75th percentile) category had a significantly low hazard risk and deer in the very poor BCI (10th percentile) category had a significantly high hazard risk. Deer with collar mass >2% of body mass also had a significantly high hazard risk.

The good body condition (BCI Good) category was most explanatory of survival ($P <$ 0.06, β = -0.62, SE = 0.33). Deer in good body condition were at a lower hazard risk (0.54, 95% CI = 0.28–1.02). Deer with collars >2% of their body mass were at a higher risk of death (1.82, 95% CI = 0.96–3.46). The best model included both variables (Table 3.7) and made the hazard ratios slightly more conservative than when individually tested (Table 3.8). This was likely caused by deer that were within both a good or poor category of body condition and had collar mass >2%. Twenty-four deer had collars >2% of body mass: 8 in poor BCI, 5 in good BCI, and 11 in mid BCI. All hazard ratios overlapped 1 and should be viewed with caution.

Body condition index did not interact with collar mass ($P > 0.42$), nor was there interaction between collar >2% of body mass and poor BCI ($P > 0.77$) or body condition index and collar >2% ($P > 0.59$).

Mean body condition of deer captured in 2007 (0.88, SE = 0.9, n = 120) differed (t_{138} = 2.25, $P < 0.03$) from deer captured in 2008 (-0.47, SE = 0.2, n = 20).

Table 3.7: Model results of Cox regression analysis

Model	*P*	χ^2	df	-2 Log L	AIC	Δ AIC	w_i
Null	-	-	0	306.30	306.30	2.84	0.07
Collar >2%	0.07	3.39	1	303.19	305.19	1.73	0.12
BCI very poor	0.06	3.53	1	303.09	305.09	1.63	0.13
BCI very poor, Collar >2%	0.04	6.41	2	300.50	304.50	1.03	0.18
BCI good	0.06	3.66	1	302.20	304.20	0.73	0.20
BCI good, Collar >2%	0.04	6.66	2	299.46	303.46	0	0.29

Table 3.8: Cox regression model parameter estimates and hazard ratios with individual parameters and combined.

Model	Label	Parameter	Hazard Ratio	95% Hazard Ratio Confidence Limits		β
1	collar and BCI good	collar >2%	1.75	0.93	3.32	0.56
		good BCI	0.55	0.29	1.04	-0.60
2	BCI good	good BCI	0.54	0.28	1.02	-0.62
3	collar and BCI very poor	lower 10% BCI	1.90	0.91	3.98	0.64
		collar >2%	1.73	0.91	3.27	0.55
4	BCI very poor	lower 10% BCI	2.01	0.97	4.18	0.70
5	collar	collar >2%	1.82	0.96	3.46	0.60

3.4.6.3.1.3 Home range subset

The null model was accepted as the best compared to models with home range covariate measures. Significance values for variables ranged from $P = 0.23$ (average elevation) to $P = 0.88$ (proportion of wetland). Most *P* values were above 0.5.

3.4.6.3.1.4 Winter severity

Winter of 2008 was more severe than that of 2007 according to temperature, snow depth, and rainfall measures (Table 3.9). These results help explain why deer captured in 2008 were in poorer body condition than those captured in 2007. Thirty-year normal data are listed where available. Summer rainfall was below normal in both years.

Table 3.9: Comparison of winter severity indicators for 2007 and 2008 and 30-year normals.

Capture year	Winter	below -20°C (days)	Snow depth >10 cm (days)	summer rainfall (mm)
2007	2006/07	30	75	238
2008	2007/08	38	93	208
-	30-yr. normal	34	n/a	352

3.5 Discussion

3.5.1 CWD Management Program

Most of the radio-collared deer died during hunting season months. Hunters were notified of the CWD research project in the annually-published Saskatchewan Hunters' & Trappers' Guide, and were asked not to shoot collared deer, but it was not illegal to do so. Twenty-four deer were shot by hunters who reported and returned the collars. We suspect some of the other deer that died during the hunting season may have been fatally wounded or not recovered by hunters. Hunters often reported not seeing a collar at the time of shooting and others indicated they had not read the related information in the guide. Some hunters reported seeing a deer with a collar and as a result not shooting. I suspect the number of radio-collared deer that were shot under-represents the hunting loss in the area, but the effect is probably marginal.

3.5.1.1 Male and female survival during the hunting season

The provincial CWD management program changed dramatically beginning in 2008. The CWD area expanded to include more management zones but permits were less liberal. The Earn-a-Buck Program was altered such that antlerless mule deer permits were no longer provided for free but at a cost of $19.62 each and the fee for an either-sex mule deer license was increased from $19.81 to $37.29. Heads from antlerless deer, submitted in order to receive an either-sex permit, were now accepted from anywhere in the province whereas previously they were required to be taken from CWD zones only. In 2007, hunters could take an unlimited number of

antlerless deer but in 2008 they were limited to 4 antlerless deer. Consequently, adult doe survivorship increased in 2008 hunt season.

The explanation for decreased survival of males in 2008 compared to 2007 is less clear. Three individuals died in autumn season 2007, and 15 in 2008; of these, 1 died by vehicle collision, 8 were hunter-shot, one was suspected to have been shot, and the cause of death for the remaining 8 were unknown as only scavenged remains were found. It cannot be assumed that autumn mortality is entirely due to hunting; however, it is likely several of the deaths of unknown-cause were a result of wounding during the hunting season. It is possible that hunters were more likely to submit the antlerless heads now that they could be harvested province-wide and more either-sex licenses were purchased as a result. The antlerless permits in 2007 included a 3-point-or-less deer, but not in 2008. This may have resulted in fewer sub-adult males in the population in 2008 and added pressure on mature males. Adult male survival during the 2007 hunt season was high considering this was a herd reduction area (0.94, SE = 0.03). Conclusions drawn from this result are limited, because only 2 years of data were available. There could be random factors at play, and factors we did not or could not measure (e.g., age structure of the herd, hunter attitudes, effect of radio collar on likelihood of harvest).

Annual survival rates of adult male mule deer averaged 0.72 (SD = 0.14), which is relatively high compared to other studies. In Montana, adult male survival rates varied from 1990 to 1995 but averaged 0.52 (SD = 0.13) and 0.57 (SD = 0.09) on 2 study areas, the latter having some private land with restricted access during hunting season (Pac and White 2007). In Idaho, adult male annual survival rates over a 4-year period starting in 1993 averaged 0.54 (SD = 0.15) (Bishop et al. 2005). Even though our study areas were within herd reduction zones with liberal deer licenses, hunting pressure in Saskatchewan remains limited by a low hunter population

relative to other regions. To date, herd reduction for CWD management has relied on incentives to increase hunting in affected areas; given these findings, alternative methods such as the use of sharp-shooters, etc. may be required to achieve desired population goals.

3.5.2 Body Condition

Body condition scores measure nutritional status of ungulates, and are good predictors of survival. Our results indicated that deer in good body condition (75^{th} percentile, $n = 37$) were more likely to survive, and deer in very poor body condition (10^{th} percentile, $n = 14$) were more likely to die. In this study, the threshold of body condition that reduces survival probability was more extreme than that which increases survival probability. In a longer study we might find that the effect of body condition on survival varies depending on other factors, such as winter severity. The lower threshold of poor body condition that affects survival might increase if circumstances were more strenuous.

Compared to 30-year normals, winters during the study period had similar numbers of days below -20°C, but snow depth data were unavailable for comparison. Summer precipitation values appeared to be below normal. However, this conclusion is based on data that may not accurately represent the study area. The central weather station at Lucky Lake did not have 30-year normal precipitation data available and the 2 other stations were quite varied from one another: 254 mm and 450 mm were the values for the Swift Current and Elbow weather stations respectively. Elbow falls in the moist mixed grassland ecoregion, which receives more rainfall than the mixed grassland ecoregion that encompasses most of the study area. These statistics might give some evidence of below normal precipitation that could affect body condition, but the evidence is not strong enough to make a valid scientific assessment.

Body condition varied between years and corresponded with measures of winter severity. Years of extreme snow depth have been related to white-tailed deer mortality from malnutrition

in Saskatchewan (Runge and Wobeser 1975), but areas where mule deer range generally have less snow accumulation due to wind and terrain.

Males were generally in poorer condition than females, which we expected because male mule deer expend their energy reserves during the breeding season and are more likely to succumb to winter starvation than their female or non-breeding male counterparts (Geist 1994a).

3.5.3 Radio Collars

Guideline 28 of the Canadian Council on Animal Care (CCAC)'s care and use of wildlife (2003) states that radio transmitter weight should not exceed 5% of the animal's body mass. Our results indicate survival effects can be seen at levels below 5% and suggest that the limit should be lowered to ~2%. Collar weight may not be the only risk factor as deer with collars between 2 and 3.4% of body mass were mostly juveniles captured in 2007 and other unmeasured factors may have contributed to the high hazard rate. The capture and collaring protocol differed between years, leaving no control to compare the treatment in 2007 and 2008. Of the deer with collars >2%, all but 1 were captured in 2007, and the one captured in 2008 was an adult. There were few adults with collars >2% of body mass. However, we encourage researchers to further investigate the effect of collars on survival and behavior and to limit collar mass to below 2% of the research animal's body mass whenever possible.

3.5.4 Home Range Habitat Effect on Survival

None of the habitat measures we evaluated affected survival. However, habitat selection occurs at multiple scales and is influenced by numerous factors (e.g., predator abundance, conspecific use of habitats, forage quality) (Klaver et al. 2008). A more specific resource-selection approach may have been more appropriate, one that measures frequency of use compared to availability (Garshelis 2000). Another approach was undertaken by Bender et al. (2007b), who related habitat selection to mule deer doe condition in New Mexico. Mortality risk

by predator species varies by habitat, especially in areas where there are large predators such as mountain lions or wolves (Bishop et al. 2005, McLoughlin et al. 2005), but can also be affected by conspecific group size. Coyotes are the largest common predator in southern Saskatchewan and it is more likely they would take down fawns than yearlings or adults. In our study areas, some lands are poorly accessible to hunters due to rough terrain or restricted access and may give protection to deer during hunting season.

3.6 Management Implications

Survival rates depict radio-collared deer in Southern Saskatchewan for a 2- or 3-year period. There were management practices in effect for the CWD program that are not in place throughout the entire province; therefore, these rates are specific only to these areas and cannot describe province-wide mule deer survival rates. We have demonstrated survival differences between adult males and females dependent on harvest regulations. In the future, managers may want to consider how survival rates changed as a result of program adjustments between 2007 and 2008 prior to making new adjustments to the program. Juvenile deer had poor survival compared to adults. The status of the population growth (or decline) cannot be inferred without fawn survival estimates.

Hazard ratios that approximate 1 indicate no effect of a covariate. Ninety-five per cent confidence intervals were near 1 at their limits for most significant parameters, and results should be treated with some caution. Hazard ratios could be more accurate if the study was repeated and/or sample sizes increased.

Wildlife survival depends on a number of factors, none of which are static. Weather factors such as winter severity play an important role in overwinter survival in deer, and a 3-year window of observation is not likely to accurately estimate the range in winter conditions or drought conditions Saskatchewan endures. These survival estimates are a snapshot in time and

should be treated as such. They will be useful in the future to compare with survival rates if CWD prevalence rates increase to a point it is affecting herd health. We recommend ongoing study of deer survival in CWD-endemic areas of Saskatchewan, with particular emphasis on the knowledge gaps of fawn survival rates and effects of CWD on survival.

CHAPTER 4
SYNTHESIS

Wildlife managers and research biologists in North America have been struggling to contain CWD since it was first found in a wild cervids in the 1980s (Williams and Miller 2002). Despite their efforts, no management agency has effectively eradicated the disease and it continues to spread geographically and increase in prevalence. At the time of its emergence in wild populations, there was little known about CWD etiology. The main course of action in North America has been to reduce deer densities where CWD was known to exist and to sample adjacent areas to detect new cases. As we gain knowledge about prion resistance to degradation and its persistence in the environment (Mathiason et al. 2009), the complexity of managing CWD in wild cervids further unfolds. Because eradication is improbable, prevention of disease is the best method to protect wild cervids.

Researchers need to identify and quantify transmission risk from multiple causes so that managers can use best available knowledge to prevent CWD in areas where it doesn't yet exist. Risks include those associated with farmed cervids, environmental contamination, and wild deer ecology. Area-specific knowledge of host movement, contact rates and types, survival, and habitat use are vital to understanding, predicting, and modeling disease transmission and spread. In Saskatchewan, CWD was first found in mule deer and prevalence in mule deer remains higher than in white-tailed deer. Our research objective was to evaluate long distance movements and survival rates of radio-collared mule deer along the South Saskatchewan River basin.

We have concluded that mule deer of any age-sex class are capable of travelling long distances and that their movements may be predicted by habitat preferences. Fifty-five per cent of juveniles emigrated a median distance of 22.8 km (SE = 13.6) and most dispersal events occurred in spring. Forty-two per cent of adults migrated a median distance of 16.0 km (SE = 2.6) and 45% of these were obligate migrants. Males and females migrated at a similar rate and similar distances, but obligate migrants were more likely to be female. In the BEEMAT study site, most (68%) of the adult deer were migrants and at the other study sites 24 to 30% were migrants. Temporary excursions averaged 9.0 km (SE = 0.8) and were frequent year-round by females and most often during autumn by males. Deer travelled long distances in a short time period: travel was completed an average 1.1 days per migration and 5.5 days per dispersal. Migration movements were significantly directional in the BEEMAT study area, and dispersal movements were not random but were not significantly directional. Long distance movement paths were associated with selection of habitats with rugged terrain and in close proximity to grassland.

Based on these results, managers should consider that deer in expansive grassland habitats are more likely to be migrants than those in fragmented habitats, and their movement orientation will follow rugged terrain and grassland habitat. In this area, the average mule deer home range size is 24.1 km^2 (SE = 1.7) (Silbernagel 2010), but the overall area that may be included in a deer's movement patterns is larger when considering seasonal, temporary, or dispersal movements. Disease transmission and spread may occur over a large scale along with deer movements. Seasonality of movements and behaviors should also be considered because deer are more likely to come into contact with one another during the winter months (Conner et

al. 2008, Silbernagel 2010) and deer in this study area tended to winter in the coulees of the South Saskatchewan River.

Autumn (hunting season) mortality is currently most predictive of mule deer survival in Saskatchewan. Juvenile survival was lower than adult. Relative to other areas, survival rates of mule deer in Saskatchewan were relatively high. Because harvest rates can be adjusted, managers should be able to maintain desired mule deer population goals even if mortality rates increase in areas of high CWD prevalence. Deer in good body condition had lower mortality rates than their counterparts in average or below average body condition. Deer with radio collars that weighed more than 2% of the animal's body weight had lower survival rates than those with lighter collars. Researchers should use the smallest collars available that meet their needs. With this knowledge of current survival trends, it will be possible in the future to assess the impact of chronic wasting disease on mule deer survival rates.

4.1 Study Limitations

We have identified mule deer migration and dispersal patterns in southern Saskatchewan. However, white-tailed deer are the more common species throughout much of the province, and transmission risks associated with their behavioral ecology should be assessed and considered. Researchers from the University of Alberta conducted a white-tailed deer research project concurrent with ours that will produce information on contacts between groups and other risks associated with CWD transmission. White-tailed deer movement patterns have been described in a game preserve in central Saskatchewan (Stewart and Runge 1985) and of adult does in an agricultural area of southeastern Saskatchewan (Brewster and Longmuir 1994). Literature and research from the United States can also be used to identify and assess risks associated with white-tailed deer.

Conclusions about juvenile survival and dispersal rates were informative but would have been improved with a bigger sample size and with more years of data. Because most of the deer were captured in 2007, there may have been factors associated with that year (e.g., weather, harvest rates) that influenced the outcome, especially of survival rates. Survival analyses with multiple years of data provide better information than short-term studies.

Body condition indices are often validated with comparison to body content from carcasses. This allows more detailed analysis of the type of body energy being stored (e.g., body water, muscle, fat) (Cattet et al. 2002, Stephenson et al. 2002). For the purposes of this study this was not necessary, but would have been more informative and useful for comparison with similar methods in the future or for comparison with mule deer from different regions.

The effect of increased hunting pressure in herd reduction areas for CWD management on mule deer movement behavior was not addressed in this study. Hunting season begins in September and peaks in November, and coincides with rutting behavior. We could not separate the effects of each on mule deer movements but in the future, a study design could include areas of varied hunting pressure for comparison of movement behaviors. Kufeld et al. (1988) found that female mule deer did not move outside their home ranges in response to hunting pressure, but did seek areas of greater cover.

4.2 Conclusion

Chronic wasting disease is ecologically complex and wildlife managers struggle to understand and balance the various ecologic, social, and economic factors associated with the disease and its management. To date, attempts to reduce transmission and geographic spread of CWD have been unsuccessful. This research has identified factors which may help explain past failures and provide guidelines for future management actions. This research begins to derive population survival estimates in CWD-endemic areas in order to predict long-term effects of

CWD on mule deer populations. In addition, this information can be used to evaluate effects and transmission of other diseases or pathogens in wild deer.

More specifically, we found that mule deer migration or dispersal movements were more frequent and extensive than previously thought. Mule deer often travel 16 to 23 km (and not infrequently up to 200 km) and are more likely to be migratory in areas with extensive grassland. They are likely to follow rugged terrain and grassland, which may help to explain the apparent westerly spread of CWD along the South Saskatchewan River basin into Alberta and would suggest further spread along river corridors and north within the Missouri Coteau. Obviously movement patterns of the host are important in understanding the spread of CWD; however, other factors need to be evaluated in order to understand the ecology of this complex disease. These factors include differential survival of dispersing animals, rates of infections in dispersers, spread of CWD by predators and scavengers, infection rates and movement of sympatric CWD-susceptible cervids, and environmental persistence, to name a few.

Survival analysis estimates in CWD management areas indicated that management programs to increase hunting pressure did not reduce survival rates below values reported elsewhere from non-herd reduction areas. Alternative methods of herd reduction will likely be needed in order to reach targets.

We found that the current guideline of <5% for radio collar mass to body mass for mule deer to be too high and that radio collars that weighed >2% of mule deer body mass negatively affected survival and recommend that researchers use transmitters below this threshold. GPS collars, relative to VHF transmitters, have larger and heavier batteries in order to obtain more precise and frequent data. Larger batteries also allow for longer tracking periods before collars need to be replaced. Researchers should carefully consider the tradeoff between data quality and

quantity and the negative effect of collar mass on the study animal's survival and welfare. As technology improves, collar mass will likely decrease and so will negative effects on the animal, but in the short-term, large heavy batteries/collars should be avoided.

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Appendix

A. Accuracy Assessment of Land Cover Map

Error matrices for classified land cover maps
All data are displayed in number of pixels unless otherwise noted

Sites: ANT, BEEMAT, SWI		**Training data**						
		Crop	Grassland	Shrub/ woodland	Wetland	total	**[3]Commission error**	**[4]User accuracy (%)**
Map	Crop	1349	1	0	2	1352	3	99.7
	Grassland	0	1676	20	5	1701	25	98.5
	Shrub/woodland	11	27	30	44	112	82	26.8
	Wetland	0	16	4	22	42	20	52.4
	Total	1360	1720	54	73	3207	130	91.3
	[1]Omission error	11	44	24	51	130		
	[2]Producer accuracy (%)	99	97	56	30	91		

Site:DOU		**Training data**						
		Crop	Grassland	Shrub/ woodland	Wetland	total	**Commission error**	**User accuracy (%)**
Map	Crop	1707	2	0	0	1709	2	99.9
	Grassland	31	119	3	0	153	34	77.8
	Shrub/woodland	42	89	284	34	449	165	63.3
	Wetland	457	48	8	4820	5333	513	90.4
	Total	2237	258	295	4854	7644	714	90.4
	Omission error	530	139	11	34	714		
	Producer accuracy (%)	76	46	96	99	90		

[1]*Errors of ommission* depict pixels that were incorrectly classed compared to known pixels of that class
[2]**Producer accuracy**: percentage of reference (training data) pixels classified correctly
[3]*Errors of commission* depict pixels with known values but were classed incorrectly
[4]**User accuracy**: percentage of classified pixels in the map that agree with reference data